

A critical reappraisal of the fossil record of the bilaterian phyla

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(Received 19 July 1999; revised 9 November 1999; accepted 13 December 1999)

ABSTRACT

It has long been assumed that the extant bilaterian phyla generally have their origin in the Cambrian explosion, when they appear in an essentially modern form. Both these assumptions are questionable. A strict application of stem- and crown-group concepts to phyla shows that although the branching points of many clades may have occurred in the Early Cambrian or before, the appearance of the modern body plans was in most cases later: very few bilaterian phyla *sensu stricto* have demonstrable representatives in the earliest Cambrian. Given that the early branching points of major clades is an inevitable result of the geometry of clade diversification, the alleged phenomenon of phyla appearing early and remaining morphologically static is seen not to require particular explanation. Confusion in the definition of a phylum has thus led to attempts to explain (especially from a developmental perspective) a feature that is partly inevitable, partly illusory. We critically discuss models for Proterozoic diversification based on small body size, limited developmental capacity and poor preservation and cryptic habits, and show that the prospect of lineage diversification occurring early in the Proterozoic can be seen to be unlikely on grounds of both parsimony and functional morphology. Indeed, the combination of the body and trace fossil record demonstrates a progressive diversification through the end of the Proterozoic well into the Cambrian and beyond, a picture consistent with body plans being assembled during this time. Body-plan characters are likely to have been acquired monophyletically in the history of the bilaterians, and a model explaining the diversity in just one of them, the coelom, is presented. This analysis points to the requirement for a careful application of systematic methodology before explanations are sought for alleged patterns of constraint and flexibility.

Key words: Cambrian, Bilateria, functional morphology, planktotrophy, trace fossils, body size, stem groups, phyla, origins, molecular clocks.

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I. INTRODUCTION

With the increasing interest in the specification of body plans in development, interest has also become directed at the evolutionary aspects of this area (e.g. Davidson, Peterson & Cameron, 1995; Arthur, 1997; Gerhart & Kirschner, 1997). Typically, the fossil record is invoked to support the following pattern: major body plans (which correlate with the extant phyla) appeared early in the Cambrian (the so-called 'Cambrian explosion'), and then persist with their essential features unchanged up until the Recent (e.g. Valentine, 1995). An alternative – and no less striking – hypothesis has been that the extant phyla diverged well before the Cambrian, but remained small and cryptic until that time (e.g. Fortey, Briggs & Wills, 1996). One final possibility has been a hybrid between the two (Balavoine & Adoutte, 1998), suggesting that some large animals were present in the Proterozoic (even before the latest Proterozoic Ediacaran biota) but have simply not been found through low diversity or rarity.

In these scenarios, given an apparent early appearance of phyla, and subsequent constraint, one is tempted to ask the question, what was special

about evolution before the Cambrian which generated so many different body plans, and why have none evolved since? In general, two different explanations for this phenomenon have been offered; that the early diversification is due to 'empty ecospace' into which early experimental phyla could expand into relatively unhindered, with access to ecological niches later in the Phanerozoic being severely restricted; or that early development was more plastic, allowing a greater degree of non-lethal experimentation, followed by developmental 'hardening' later in the Phanerozoic which greatly restricted evolutionary potential (see Valentine, 1995 for review and discussion). Here, we will discuss a third alternative, that the generally accepted view of the phyla appearing at the latest by early in the Cambrian is not supported by the fossil record, and that the possibility of body plan innovation occurring throughout the Phanerozoic cannot be discounted. To do so requires exploiting the important difference between cladogenesis and the origins of the features of modern phyla (see Fortey *et al.*, 1996 for a somewhat similar discussion but coming to radically different conclusions).

The data that would be required to resolve these

issues seem to be as follows: first, what are relationships between extant phyla, and how do fossil taxa fit into this scheme? Much of the early fossil record of bilaterian evolution comes from the latest part of the Proterozoic some 570–545 million years ago (Ma); fossils from this period are highly controversial and thus require careful consideration [at present, the terminal Proterozoic system has not been formally named or defined. However, the common usage of Vendian and Ediacarian closely matches the likely definition placing the base of the system at or close to the end of the Marinoan glaciation (Kennedy *et al.*, 1998)]. Secondly, what ecological and functional constraints are placed on animals by the evolution of certain types of morphological feature such as segments and coeloms? Thirdly, does the nature of the Cambrian fossil record actually support the contention common to all three of the ecology/developmental constraint/poor discovery rate hypotheses, namely that the extant phyla do appear suddenly at the base of the Cambrian? Most importantly though, the question of what a phylum actually is needs to be addressed.

II. WHAT, IF ANYTHING, IS A PHYLUM?

Although the debate about the origins of phyla has been vigorously conducted, there has been surprisingly little debate about the very terms of enquiry: how is a phylum defined, and how would variations in its composition change the nature of the debate? (See Valentine & Hamilton, 1997 for a useful exception.) There is, in fact, a difference between those who see a phylum as ‘a group of species sharing a common organization of the body’ (Adoutte *et al.*, 1999, p. 104) and those who see a phylum in phylogenetic terms, although the problem is concealed by the common assumption that members of a phylum are in some way united by a body plan. Nevertheless, in the extant fauna, phyla appear to be used as the largest groupings of taxa that can readily be seen to be more closely related to each other than to any other groups: a primarily taxonomic or phylogenetic usage rather than a morphological, ‘body plan’ based one [for some phyla are recognized to include highly aberrant members, such as the pentastomids (Abele, Kim & Felgenhauer, 1989), or *Xenoturbella* (Israelsson, 1997; Norén & Jondelius, 1997)], although, critically, such assessments have generally been based on morphology. Claims that the phyla are characterized by particular types of ‘body plan’ features which

putative super-phyletic groupings do not possess (e.g. see Table 2-2 in Arthur, 1997) thus seem to be based on an artifact of how we classify groups of animals: if such ‘super-phyletic’ features were readily identifiable, the larger grouping would itself probably be called a phylum, as it would be recognized to be phylogenetically unified. As the level at which this ignorance of relationships becomes important is likely to vary between groups, the cladist’s standard criticism that phyla (and other such ranks) should be positively discouraged on the grounds that they engender spurious comparisons between members of the same ‘rank’ (see e.g. Smith, 1994, and references therein) seems to be valid.

Whilst phyla are often satisfactory and coherent groupings, an important corollary of this usage is that phyla are defined in such a way that virtually guarantees we are ignorant about their inter-relationships. Indeed, morphologically distinct groups of taxa that nevertheless do show clear affinities to one or other of the major phyla (such as the onychophorans, tardigrades, acanthocephalans, pogonophorans or echiurans) present a problem for the phylum concept (Budd, 1998*a*). Such groups are sometimes referred to as arthropods, rotifers or annelids, and sometimes as phyla in their own right. Such difficulties demonstrate the tensions that arise from trying to think about phyla in both phylogenetic terms and in terms of a group of taxa which share a particular ‘body plan’. Given that the phyla have an evolutionary origin, their characters – and thus their body plans – must in broad terms have been assembled in a particular order (Valentine & Hamilton, 1997; Budd, 1996, 1998*a*). There is thus a logical decoupling between the body plan that the extant members of a phylum share, and their phylogenetic affinities to each other, even when they are tightly correlated with each other in the extant fauna. Early in the history of a clade, when the body-plan features of a group had in the main yet to emerge, members of sister-group lineages of different clades must have been very similar to each other (see e.g. Erwin, Valentine & Jablonski, 1997). This distinction is crucial, because confusion between the phylum considered as a phylogenetic grouping and as a group of taxa that share a body plan has led to considerable misinterpretation of the evolutionary origins of phyla.

The differences between that group of organisms most closely related to a particular extant phylum and the members of that phylum itself have been formalized into the stem- and crown group concepts (Jefferies, 1979; Fig. 1), which allows a more precise

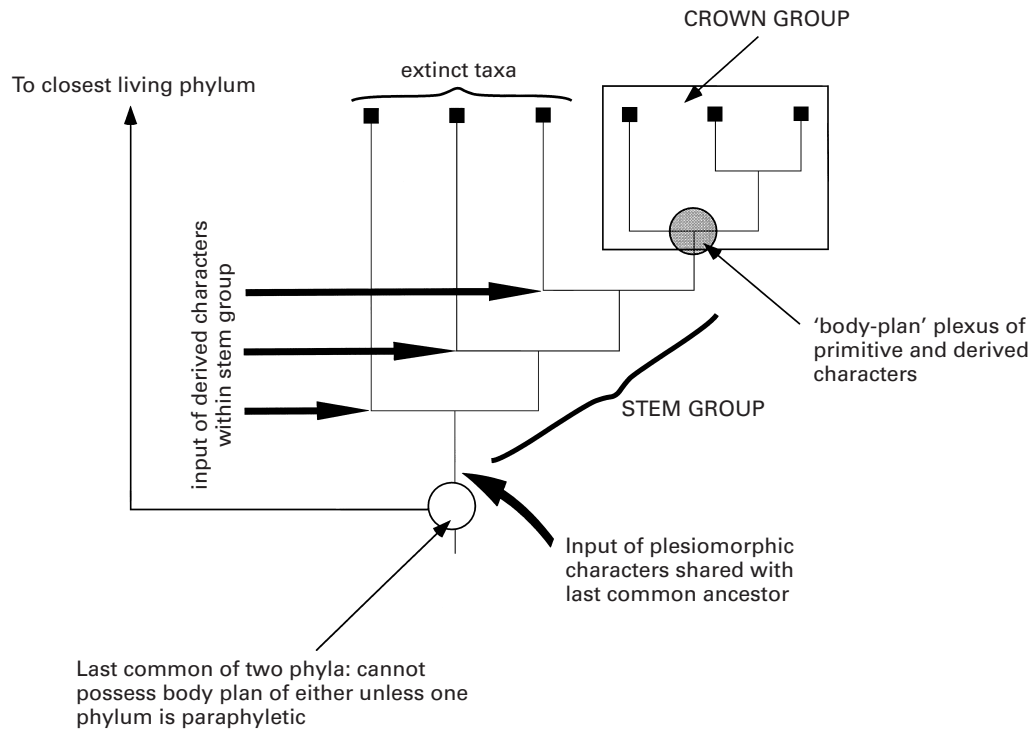


Fig. 1. The stem- and crown group concepts and the origin of the body plan (modified from Budd, 1998a). The crown group of a phylum consists of the last common ancestor of all living forms in the phylum and all of its descendants; the stem group consists of a series of entirely extinct organisms leading up to the crown group away from the last common ancestor of this phylum and the most closely related phylum. On this view, there cannot be an 'extinct' phylum with an extinct body plan. The body plan cannot originate at the same point as the clade does, because at this point the organisms in question are identical for pairs of most closely related phyla: the view defended herein is that the origin of the body plan should be identified with the origin of the crown group.

definition to be given to a 'body plan'. Although various alternatives are available for the definition of a body plan (Valentine & Hamilton, 1997), such as attainment of the characteristic developmental programme or morphology, we defend here a phylogenetic criterion: a body plan is that set of features plesiomorphically shared by extant taxa in a monophyletic clade. This is a useful definition for two reasons. First, it conforms precisely to the common-sense view of a 'body plan' as something shared by living groups of animals, and secondly it is a totally objective definition that does not require any subjective assessment of the 'importance' of various body features. This subjectivity has in the past led to such elasticity in the concept that it has become virtually devoid of meaning. This restriction of the body plan to extant taxa enables the concept to be used usefully without the problems caused by basal members of stem groups which may differ little from members of closely-related stem groups. Apart from at the origin of the entire clade, the only other objective point that can be fixed in a clade is the origin of the crown group. Thus, in the view adopted

here, the body plan of the extant members of a phylum can be traced back only to the origin of the crown group. The most basal members of the stem group are virtually identical to basal members of the stem group of the closest living phylum and as such cannot be said to possess a distinctive 'body plan' of one or other of the two phyla.

As discussed by Runnegar (1996), this distinction leads immediately to an important point of principle: the time of divergence of a clade should not be confused with the time of appearance of the body plan (considered here equal to the origin of the crown group): a point that is valid no matter what the imperfections of the fossil record are. As we aim to demonstrate below, this confusion has led to conceptual difficulties in dealing with the origin of phyla, with the main outcome being consistent overestimation of the time of their origin.

Stress on the stem group of a phylum is important because it is an evolutionary 'space' within which major reorganizations of the body can take place, such as in the cases of the arthropods (Budd, 1996, 1997, 1998a, 1999b) and echinoderms (Mooi, David

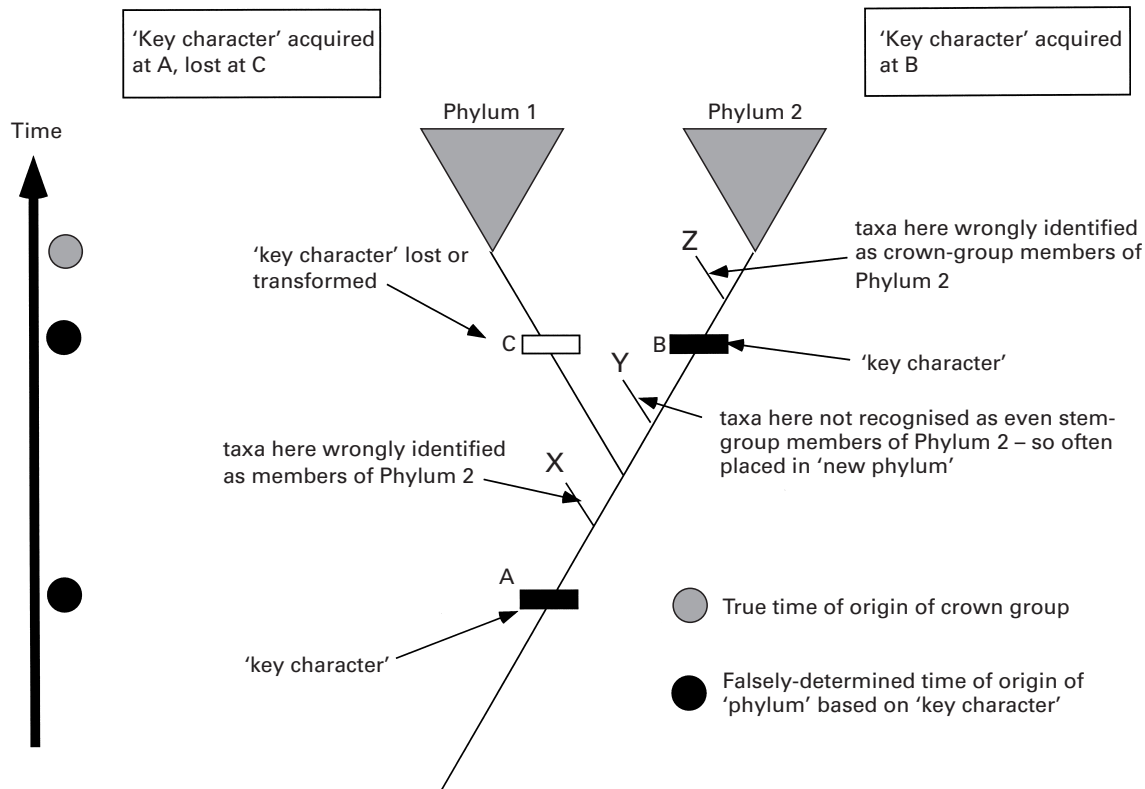


Fig. 2. Mistakes caused by the failure to recognise the stem/crown group distinction. Labels on the left of the diagram refer to a supposedly key character (e.g. the echinoderm stereom) that has been gained in the stem group to two phyla at point A, and lost at point C in the stem group of Phylum 1: Taxon X is misidentified as belonging to Phylum 2 (in this case the echinoderms) because it possesses the supposed key character. The 'phylum' will be supposed to have originated much deeper than the crown group. Labels on the right of the diagram refer to the key character being gained at point B. Taxon Y will be misidentified as an 'extinct phylum' or conceivably a member of Phylum 1 if it retains many plesiomorphies, and its relationship to Phylum 2 may typically be missed. Taxon Z will be referred to 'Phylum 2' and the origin of the body plan will be placed too early. Note that in all cases the origin of the body plan is mistakenly placed too early (time line on far left).

& Marchand, 1994): neglect of this possibility leads, *in extremis*, to the curious view that during divergence, 'phylum level' differences appear first, followed by 'class level', 'order level' and so on (Willis, 1940; Gellon & McGinnis, 1998; Budd, 1999a). There is no particular reason to think that major differences in organization or development occur early in a clade's history, and indeed, given the degree of preadaptation probably required to prepare them, a later appearance might be more normal (but see also Erwin, 1993). As members of stem groups inevitably resemble one extant phylum more closely than another (or perhaps one group of phyla more than another), and that logically, any fossil organism that does not fall into an extant phylum must fall into a stem group to a phylum or group of phyla, the appearance of animals resembling members of extant phyla in the Cambrian

is hardly surprising (cf. Fig. 2). However, from the above it can be seen immediately that this mere recognition is not enough to establish the origin of the extant body plan, even if the animal in question seems quite similar to the extant forms. Typically, it is the possession of a single character such as the stereom structure in echinoderms or segmentation in arthropods that allows this assignment, a procedure that suffers from three flaws (Fig. 2). First, it makes the assumption that one character can in fact stand proxy for the entire complex of characters present in the extant body plan. This might be true if body plans were indeed immutable complexes, so internally constrained that they could not have been acquired piecemeal: but this assumption does not seem to be correct, not least because the fossil record can be employed to demonstrate how this assembly took place (e.g. Budd, 1998a). Secondly, by

insisting on a particular character, it may fail to recognize stem group members that have yet to acquire it. For example, if the stereom structure was acquired within the echinoderm stem group, then logically there must exist stem group members that do not possess it. They are thus unlikely to be regarded as echinoderms of any sort. Indeed, these sorts of taxa (such as the stem group arthropods *Opabinia* and *Anomalocaris*) have typically been assigned to their own 'phylum' on the grounds that, in this case, they do not possess supposed key diagnostic characters of the arthropods such as the sclerotized exoskeleton. Thirdly, this view fails to recognize that characters may in fact have had a wider distribution than they do today, and thus may have been acquired in the stem groups to at least pairs of phyla, only to be lost in one of them (this possibility underlies the 'calcichordate' controversy, with the theory claiming in effect that the calcitic skeleton possessed now by the echinoderms had a wider distribution in the past, and was in fact present in the stem-lineage to the chordates; see Gee, 1996 for discussion). If this failure of recognition occurs, animals that belong deep down in phylogeny will be wrongly assigned to an extant phylum. The existence of stem groups – a uniquely palaeontological concept – means that the neontological terminology of 'phyla', especially when taken to be synonymous with 'body plan', should only be applied to the fossil record when carefully qualified. Recognition of the importance of stem groups is thus essential: loosely referring to taxa as 'arthropods', 'annelids' or 'priapulids', and referring taxa to these entities on insufficient grounds can obscure as much as elucidate evolutionary relationships and the pattern of body-plan emergence.

Demonstration of crown-group rather than stem-group affinities of an organism may be difficult, as it relies on demonstration of at least one synapomorphy shared with a member of an extant sub-group of the phylum in question. In other words, the taxon in question must be shown to lie either in an extant sub-grouping of a phylum, or in the stem group of such a group. Naturally, this in turn will often rely on an adequate understanding of crown group phylogeny and especially rooting – knowledge that is rarely referred to in body-plan evolution discussions. Armed with this insight, it is possible to reexamine the fossil record of key taxa with a view to distinguishing between clade and crown group origins. In the following discussion, we are not aiming to present a definitive picture of Cambrian systematics. Rather, we wish to point to the controversial aspects of it,

and to note how conservative a reading of the fossil record is permitted by this uncertainty.

(1) Arthropods

Early Cambrian material from Poland reveals the anomalocaridid-like *Cassubia* (Dzik & Lendzion, 1988), a stem-group arthropod (Budd, 1997), together with the nektaspid *Liwia*. Given that nektaspidids are likely in formal terms to belong in the stem-group of chelicerates (see Edgecombe & Ramsköld, 1999; Walossek & Müller, 1990 for discussion of this area of arthropod systematics), an assignment to the euarthropods is likely. Crown-group arthropods are thus likely to have emerged by the base of the Atdabanian (see Fig. 7 for a provisional timescale and stratigraphic sequence for the Cambrian). Their presence before this time is less certain. The earliest trace fossil that can be assigned to a crown-group arthropod is probably *Rusophycus*, which is present at least by the beginning of the Tommotian (Crimes, 1987) and, depending on correlation, may be present in the underlying Nemakit-Daldynian. Despite this early appearance of the crown group, however, recent revisions of arthropod phylogeny and fossil assignment bring into question the presence of any crown-group members of extant classes during the Early and Middle Cambrian. Although stem-group crustaceans are known from the Early Cambrian (Hinz, 1987; Hou *et al.*, 1996; Walossek & Müller, 1998), the oldest crown-group taxa appear to be from the Late Cambrian [including the well-described *Rehbachella* from the Orsten fauna (Walossek, 1995)], a view of crustacean origins supported by the data (but not their interpretation) of Walossek (1999), a recent review of the subject. *Canadaspis*, the supposed phyllopod from the Middle Cambrian Burgess Shale (Briggs, 1978) is now widely considered not to be a phyllopod or even a crown-group crustacean (Dahl, 1984; Boxshall, 1997; but see also Briggs, 1992). The entire Cambrian record of ostracods, known largely from bivalved carapaces of taxa such as the bradoriids (Siveter & Williams, 1997), has also been thrown into considerable doubt by the description of the soft-part anatomy of *Kumingella* from the Early Cambrian Chengjiang fauna (Hou *et al.*, 1996). Similarly, the Cambrian record of crown-group chelicerates is suspect, with the Burgess Shale *Sanctacaris* (Briggs & Collins, 1988) being now considered to be in the arachnate clade (and thus a stem group chelicerate) rather than in the crown group (Dunlop & Selden, 1997). Finally, the old concept of the Uniramia, uniting insects with

myriapods and onychophorans, which in *Aysheaia* (Whittington, 1978) had a putative member from the Middle Cambrian (Gould, 1989) is now defunct, and in any case *Aysheaia* itself is probably best considered not to lie in even the onychophoran stem lineage (Budd, 1996; but see also Ramsköld & Hou, 1991 and Ramsköld & Chen, 1998 for an alternative view of the latter). The entire known fossil record of arthropods up to the Late Cambrian thus seems to consist of forms lying either in the stem group of the entire clade, such as *Anomalocaris* and *Kerygmachela* (Fig. 3A), or in stem groups of extant clades within the crown group. It is already clear that a great amount of body-plan reorganization must have taken place post Cambrian, to generate such distinctive taxa as for example the spiders and flying insects.

(2) Priapulids

Although it is commonly agreed that the Burgess Shale taxa such as *Ottoia* and *Selkirkia* are 'priapulids' (following Conway Morris, 1977), they do not fulfil the criteria laid out above: the fact that they 'share characteristics with both [extant] orders' and the sobriquet 'archaeopriapulids' (Conway Morris, 1977) tacitly recognizes this, together with the suggestion that the most basal extant priapulid is in some ways morphologically intermediate between the Cambrian and extant examples. The recent analysis by Wills (1998) is consistent with the view that the extant priapulids are all more derived than any Cambrian example. Even if extant priapulids cannot be shown to share a synapomorphy that distinguishes them from the Cambrian forms, this is, as discussed above, not enough to demonstrate that the Cambrian forms do indeed lie in the crown group. The demonstration of the existence of other large, but probably not priapulid worms in the Cambrian which are nevertheless cycloneuralians (i.e. the palaeoscoleids, see below) strongly suggests that many 'priapulid' features such as the large size, introvert and annulated body are actually inherited plesiomorphies from a deeper ancestry. The actual origins of the priapulid crown group are uncertain. The Carboniferous form *Priapulites konecniurum* (Schram, 1973) shows considerable affinities to the extant family Priapulidae, so that the fossil record can place a minimum age of Pennsylvanian on it.

(3) Other 'aschelminths' or 'ecdysozoans'

The Cambrian fossil record yields various taxa that might reasonably be assigned to the 'Ecdysozoa'

(Aguinaldo *et al.*, 1997) or at least the Cycloneuralia (Nielsen, 1995). Prominent among these are various annulated animals with conspicuous cuticles, such as the palaeoscoleids and similar taxa from the principal Cambrian *Fossil-Lagerstätten* (Hou & Bergström, 1994; Fig. 3B). Many of these taxa are known to possess an armoured proboscis. However, such a feature is widespread in extant cycloneuralians and is not necessarily diagnostic for any particular group. The presence of these large forms is of interest because it has been widely considered that the ground-plan of all the Cycloneuralia was a rather small animal, suggesting that the large animals such as the priapulids are secondarily so (e.g. Schmidt-Rhaesa *et al.*, 1998).

(4) Annelids

Although Clark (1964) argued for an oligochaete origin for the annelids, the balance of opinion today leans heavily towards a concept of the polychaetes being both basal and also paraphyletic, giving rise not only to other annelids but also to the echiurans, myxostomids and pogonophorans (e.g. Nielsen, 1995; McHugh, 1997). Recognition of a broadly polychaete-like habitus is thus not sufficient evidence to allow assignment of a fossil to the crown group (unlike recognition of an oligochaete habitus, for example). Annelid-like worms have been recognized from the Cambrian, including the famed polychaetes from the Burgess Shale (Conway Morris, 1979; Fig. 3C), and the North Greenland Sirius Passet fauna (S. Conway Morris, personal communication). These taxa typically possess paired bundles of setae, and in general appear very like polychaetes. Nevertheless, none of the Cambrian forms can be related easily to any extant forms, and the apparent complete lack of sclerotized jaws suggests (but does not necessarily imply) that all of the Cambrian examples are more basal than the last common ancestor of all living annelids. Furthermore, the anterior end of the fossil examples differs considerably from that of extant forms – there appears to be no peristomium, for example (R. A. Dewel, personal communication). The first annelid jaws appear in the fossil record in the Early Ordovician (Benton, 1993), and it must be supposed that this represents a maximum age for the origin of crown-group annelids. Possibly jaws evolved before the last common ancestor of the extant annelids, in which case the crown group could have evolved considerably later than this. The polychaete-like features of the Cambrian forms may have a much broader

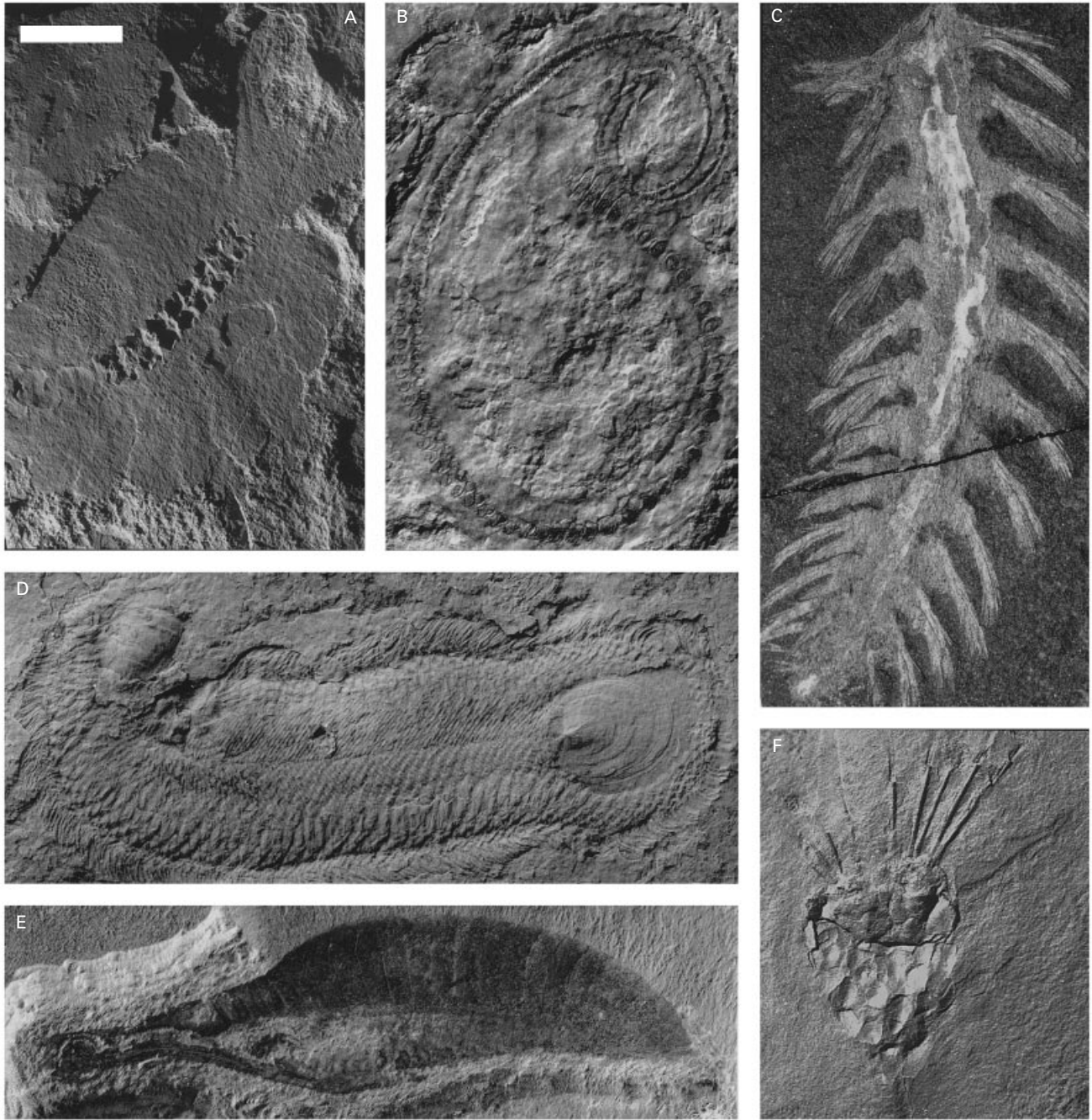


Fig. 3. Candidate taxa lying in the stem groups of phyla or of groups of phyla. (A) *Kerygmachela* from the Early Cambrian Sirius Passet fauna, a stem-group arthropod; (B) *Cricocosmia* from the Early Cambrian Chengjiang fauna, a potential stem-group cycloneuralian (photograph courtesy of Hou Xianguang & J. Bergström); (C) *Burgessochaeta* from the Middle Cambrian Burgess Shale, a stem-group annelid (photograph courtesy of S. Conway Morris); (D) *Halkieria* from the Early Cambrian Sirius Passet fauna, a stem-group lophotrochozoan (i.e. the clade including annelids, molluscs, sipunculans and brachiopods) (photograph courtesy of J. S. Peel); (E) *Yunnanozoan* from the Early Cambrian Chengjiang fauna, a potential stem-group deuterostome (photograph courtesy of Hou Xianguang & J. Bergström); (F) *Gogia* from the Middle Cambrian Spence Shale, a possible stem-group echinoderm (specimen courtesy of S. Conway Morris; specimen number SM X.29434, deposited in Sedgwick Museum, Cambridge, UK). Scale bar length: (A) 12 mm; (B, C) 4 mm; (D) 7 mm; (E, F) 5 mm. See text for further details.

phylogenetic distribution than the annelid clade, as implied by Conway Morris & Peel (1995); the setae and overall form are inherited plesiomorphies that do not in themselves indicate an annelidan affinity.

(5) Echinoderms

Crown-group systematics of echinoderms are in a state of flux, but the origin of the crown group would appear to be defined by the last common ancestor of pelmatozoans and eleutherozoans. When this animal lived is controversial, and depends very much on the systematic position of some controverted Cambrian fossils. The earliest fossil that has been assigned to the echinoderms is *Arkarua*, from the terminal Proterozoic of Australia (Gehling, 1987). However, although this fossil possesses pentaradial symmetry, its small size, combined with preservation in relatively coarse sand means that other echinoderm-specific features are not readily visible. Its assignment to the Echinodermata thus largely rests on this single character, and must be at present regarded as an open question. A similar argument applies to the characteristic terminal Proterozoic form *Tribrachidium* (Glaessner & Wade, 1966) which is not pentaradial. Turning to the Phanerozoic record, the first appearance of the crown group is dependent on which view of echinoderm systematics is taken. On one view, taxa such as *Gogia* (e.g. Durham, 1978; Fig. 3F) are stem-group crinoids, and thus crown-group echinoderms had evolved already by the latest Early Cambrian. Conversely, a recent phylogenetic reconstruction places all Cambrian forms in the echinoderm stem group (Mooi *et al.*, 1994; David & Mooi, 1996), implying that the crown group did not appear until early in the Ordovician. The matter is complicated by one of the key Middle Cambrian taxa, *Echmatocrinus* being argued over at some length: if it is an echinoderm, its affinities lie with the crinoids (Sprinkle & Collins, 1998) but it has also been described as an octocoral, or at least a cnidarian (Conway Morris, 1993; Ausich & Babcock, 1998). Cambrian echinoderms are morphologically diverse and appear to be united largely by plesiomorphies. The origins of crucial echinoderm characters such as the stereom had clearly taken place by the Early Cambrian; but the origin of other features such as the water vascular system (WVS) is less clear, although all known echinoderms probably possessed one (Nichols, 1972). Indeed, Nichols (1972) argues that the affinities of the WVS lie with lophophorate structures known from hemichordates (the pterobranchs) and thus may predate the origin of

the calcitic endoskeleton or even the entire echinoderm clade. No taxa have been assigned to the stem group of echinoderms which do not possess the calcitic exoskeleton, but on any reading of deuterostome phylogeny the echinoderm form is likely to be derived from a bilaterally symmetrical, worm-like animal, perhaps like the extant enteropneusts (see e.g. Salvini-Plawen, 1998). In any event, reconstructions of echinoderm phylogeny with the Cambrian forms lying in the stem group demonstrate considerable and progressive morphological innovation taking place during this time.

(6) Brachiopods

Crown-group brachiopod phylogeny is again problematic. On the assumption that the brachiopods are monophyletic (rather than polyphyletic: see discussion in Rowell, 1982 from a morphological point of view), the crown group appeared sometime in the Cambrian. In the phylogenetic reconstruction of Holmer & Popov (1996), the earliest crown-group forms (e.g. the obolids) are from the Atdabanian: the earliest articulates (as orthids) appear in the record at around the same time (e.g. Rowell, 1977). The earliest known brachiopods, the paterinids from the Tommotian of Siberia (Pelman, 1977) fall outside the crown group and indeed their musculature and mantle canal system differs considerably from other lingulate brachiopods.

(7) Molluscs

Molluscs are perhaps the most difficult phylum to deal with. Their crown group systematics is considerably complicated by the existence of the shell-less aplacophorans (e.g. Scheltema, 1996) which have been variously suggested to be paraphyletic and basal, monophyletic and basal, or derived. If aplacophorans are indeed basal, then all conchiferan (in the sense of shell-bearing, not the formal taxonomic unit) molluscs belong to the crown group. However, there are cogent reasons for doubting this reconstruction. The first is that the simple morphology of aplacophorans has been assumed to be primitive on the grounds that they are most like the flatworms, also often thought to be basal within metazoan phylogeny. If flatworms are removed from a basal position though, then there is much less impetus for considering flatworm-like morphologies in extant taxa as being basal. This view is reinforced by the recent phylogenetic reconstruction of Conway Morris & Peel (1995) who place halkieriids *s.l.* (Fig.

3D) in the stem lineages of a range of protostome taxa, including the molluscs, annelids and brachiopods. It is probable in this view that the sipunculans should also be derived from a halkieriid-like ancestor, given their broadly molluscan development. Surprisingly, halkieriids possess a large valve at each end of the body; and this bivalved condition may be primitive for all of these phyla, implying that the valves of brachiopods, sipunculans and probably the fossil hyoliths are all homologous (see Runnegar, 1996 for a forthright discussion of these and other issues surrounding stem- and crown-group molluscs). If a conchiferan condition is considered to be primitive within the molluscs, then the timing of the origin of the crown group depends both on what phylogenetic reconstruction is used, and also on the interpretation of some Early Cambrian fossils. One further complication is provided by the polyplacophorans, which do not, apparently, have a fossil record until at least the Late Cambrian (Qian & Bengtson, 1989, Conway Morris & Chen, 1991; *contra* Yu, 1984, 1987, 1990). If polyplacophorans are derived from within a univalved ancestor, then this late appearance is explicable; if not, the mollusc crown group would have originated before the first known conchiferans. The fossil record itself has generated sharp controversy (Yochelson, 1981; Peel, 1991*a, b*; Runnegar, 1996; Runnegar & Pojeta, 1992), to which the reader is referred for the sometimes complex details. Nevertheless, the controversy essentially consists of two broad schools: one, that the Early and Middle Cambrian provide examples of at least stem group forms of extant classes [e.g. *Aldanella* for the gastropods; *Fordilla* for the bivalves; perhaps *Scenella* for the cephalopods (see Fig. 6.5 in Runnegar, 1996)]. Conversely, such a reconstruction is denied to varying degrees, with the most extreme resistance provided by Yochelson (1979) and more moderate criticism by Peel (1991*a, b*). The spreading of the stem-/crown- group distinction has provided some means for moving beyond a sterile is/is not a bivalve etc argument. Nevertheless, considerable problems remain, because in the putative stem-group forms, there are almost invariably only few characters available for uniting them with the relevant crown groups. For example, in the reconstruction of Runnegar (1996), the stem-group bivalve *Fordilla* is considered to be so because of three characters: bivalved larval and adult shell (distinguishing them from the stenotheccoids, which have a univalved larval shell (Runnegar & Pojeta, 1992); opisthodontic ligament; and loss of radula, of which the latter is

presumably an inference for the fossil material. If *Fordilla* and its relative *Pojetaia* (Runnegar & Pojeta, 1992) are truly stem-group bivalves, then the apparent lack of bivalves in the rest of the Cambrian is surprising, especially as this gap constitutes a unique lacuna in the otherwise excellent fossil record of this class (Harper, 1998; see also discussion in Waller, 1998 and Geyer & Streng, 1998, which provides an example of a new probable early Middle Cambrian bivalve, *Arhouiella*, as well as the youngest known example of *Pojetaia*). Furthermore, the monoplacophorans, often considered to represent the closest available approximation to the 'hypothetical ancestral mollusc' (Wingstrand, 1985) have been attacked for being paraphyletic or polyphyletic (Peel, 1991*a, b*) partly because 'monoplacophorans' has been used in a very wide sense for cap-shaped Cambrian fossils, and also because the relationship between extant monoplacophorans and the Cambrian forms is uncertain. Various Early and Middle Cambrian taxa have been considered as gastropods (e.g. *Aldanella*), but perhaps inevitably, such an assignment relies on characters like 'coiled shell'. If such forms did indeed lie deep within the gastropod stem lineage, then one would expect only a few characters to unite them with the crown group. However, even this is problematic, because some authors (Golikov & Starobogatov, 1975; Haszprunar, 1988) have suggested that the ancestor of the gastropod crown group was limpet-like, not coiled (see Peel & Horny, 1999 for discussion of early Palaeozoic limpet-like forms). Runnegar (1996) dislikes such a reconstruction because it fails to accord with the presence of coiled 'stem-group gastropods' in the Cambrian fossil record – but this seems to be a circular argument: they are only considered to be stem-group forms because they *are* coiled.

Without reliable phylogenies of both extant and fossil taxa, these questions are unlikely to be resolved quickly, and in many ways the molluscs represent the richest and most complex problems of all taxa in the Cambrian. Such problems have nevertheless often been side-stepped by referring to the problematic forms either as members of extant classes or as 'extinct classes'. Whilst it is not possible to come to any firm conclusions concerning molluscan crown group origins, the evidence available at present suggests on balance that the crown group had already evolved by the beginning of the Tommotian. Nevertheless, an austere view of the early record of molluscan evolution would be that no absolutely demonstrable crown-group forms are known before

the Late Cambrian, with the helcionelloid-like molluscs known from the earliest record lying in an as-yet unresolved plexus of stem-group forms from which the various crown-group taxa began to emerge at the end of the Cambrian.

(8) Chordates

The presence of *Cathaymyrus* (Shu, Conway Morris & Zhang, 1996a) and *Pikaia* (see discussion in Conway Morris, 1998c) in the Early Cambrian Chengjiang fauna and the Middle Cambrian Burgess Shale fauna, respectively, both of which show broadly cephalochordate structure, suggests that chordates (considered here as cephalochordates + craniates) had evolved deep in the Cambrian or before (see also Simonetta, 1988; Simonetta & Insom, 1993; Chen *et al.*, 1995; Smith, Sansom & Repetski, 1996 for some other possible early chordates). Nevertheless, a note of caution must be sounded. First, in terms of body plan, the extant cephalochordates share few characters with the craniates, and although they are conventionally included in the same phylum, they present one of the cases where the entire group is not united by a distinctive 'body plan' (a similar case can be made for molluscs and the urochordates, which are considered as distinct from the chordates here, in line with Valentine, 1995). The story of the origin of the vertebrate body plan from the end of the Cambrian onwards is, conversely, one of the best examples of combining evidence from fossils and extant taxa to demonstrate the effects of progressive adaptation. Secondly, given the continuing controversy over chordate and deuterostome relationships (Halanych, 1995; Halanych *et al.*, 1995; Gee, 1996; Salvini-Plawen, 1998; Wada, 1998; Lacalli, 1999), mere demonstration of a cephalochordate habitus is not sufficient to demonstrate membership of the chordate crown group – the characters in question may have a broader distribution than the crown group or even the entire chordate clade. *Cathaymyrus* and *Pikaia* have not been shown to possess any autapomorphies with the extant cephalochordates, and must therefore be considered to form an unresolved polytomy with them and the craniates. However, two taxa from the Early Cambrian of China, *Myllokunmingia* and *Haikouichthys*, have recently been described as vertebrates (Shu *et al.*, 1999). The precise systematic position of these intriguing forms remains to be fully explored (Janvier, 1999), and their morphology presents some difficulties [such as in the orientation of the fin-ray in *Haikouichthys* (Shu *et al.*, 1999)], but it is nevertheless

likely that either they or *Cathaymyrus* and *Pikaia* represent crown-group chordates, which must therefore date back to the Botoman. Even in the unlikely event of none of these forms proving to be crown-group chordates, the euconodonts, now generally considered as craniates if not vertebrates (Donoghue, Purnell & Aldridge, 1998) should also be considered to be crown-group chordates, appearing in the Late Cambrian. A case for the paraconodonts being a broadly paraphyletic assemblage from which various euconodont lineages emerged can be made, but the issue remains presently unresolved (Szaniawski & Bengtson, 1993). Paraconodonts, broadly considered, range through much of the Cambrian, but their taxonomy stands in need of considerable attention (P. Donoghue, personal communication).

(9) Hemichordates

Hemichordates represent further difficulties, in that they may not represent a monophyletic group: the characters that unite the pterobranchs and enteropneusts may be plesiomorphies (see chordate references, above). If so, then there is no 'hemichordate body plan', as the two extant groups taken together merely represent the remnants of a paraphyletic grade of organization (Nielsen, 1995; Shu *et al.*, 1996a). Taking each group separately then, the enteropneusts have been reported to be represented in the Burgess Shale by '*Ottoia tenuis*' (Conway Morris, 1986), but this species has never been redescribed. Even if it possesses an enteropneust habitus, it is conceivable that this may characterize the entire stem group of the deuterostomes, and thus is not in itself enough to demonstrate strict enteropneustan affinities. Similarly, *Yunnanozoan* (Fig 3E; Hou, Ramskold & Bergström, 1991; Chen *et al.*, 1995; Dzik, 1995; Shu, Zhang & Chen, 1996b; Bergström *et al.*, 1998) has been described as a hemichordate, chordate, or neither. If it possesses deuterostome characters, it may lie deep within the clade. By the Middle Cambrian, though, very *Rhabdopleura*-like pterobranchs are known from Sweden (Bengtson & Urbanek, 1986) and from Siberia (Durman & Sennikov, 1993). By this time, then, at least the pterobranch body plan appears to have evolved.

(10) Other phyla

A host of other bilaterian phyla have been claimed to exist in the Cambrian including the pogonophorans (Sokolov, 1967), the chaetognaths (Szaniawski, 1982), the phoronids (Fenton & Fenton, 1934) and

the sipunculans (Runnegar *et al.*, 1975). Some of these claims rest on trace fossil evidence and must therefore be considered unreliable; others (such as the assignment of the protoconodonts to the chaetognaths) rely on a single character and thus fail once more to make the stem-/crown-group distinction.

(11) Discussion

As the above comments aim to show, the commonly held view that the extant phyla all appear (or can be inferred to have appeared) at the base of the Cambrian appears to be incorrect. Rather than 'unambiguous fossil representatives' of the phyla appearing then (e.g. Balavoine & Adoutte, 1998), the bulk of phylum-level body-plan evolution seems – from the fossil record – to have taken place within the Phanerozoic. Most phyla do not appear at all in the Cambrian record, and of those only a few have undoubted crown-group representatives at or near the base (arthropods by at least the Tommotian; brachiopods by the end of the Atdabanian; probably chordates; perhaps molluscs). As a corollary, given that the emergence of crown groups can be documented to a degree within the Cambrian or later, a Proterozoic origin of at least crown groups may be ruled out in the vast majority of cases.

Nevertheless, it is clear that many bilaterian lineages had diverged by the beginning of the Cambrian. What sorts of animals were undergoing this cladogenesis? The recent emphasis on the 'zootype' (Slack, Holland & Graham, 1993) has led to consideration of a so-called 'Urbilateria' which, based on the genetic machinery it seems to have possessed, is suggested to have been a complex animal (de Robertis, 1997; Knoll & Carroll, 1999). A more traditional view – in the Anglo-Saxon world at least – would be that the ancestral bilaterian was a flatworm-like animal, perhaps with some sort of body cavity (Valentine, 1994; Gerhart & Kirschner, 1997; cf. Ruiz Trillo *et al.*, 1999). In this case, body-plan features such as the through gut, coelom and blood vascular system (BVS) would have evolved repeatedly in different lineages (see discussion in Erwin, 1999). Whatever the morphology of the ancestral bilaterians, we wish to stress here that the idea of all stem-group bilaterians being referable to the same sort of entity should be strongly resisted: in the stem lineages to groups of phyla, as in the phyla themselves, character acquisition is likely to have been a hierarchical and divergent process. The phyla clearly did not each originate from the same sort of animal [such as Gerhart and Kirschner's

(1997) 'Roundish Flatworm', a concept developed from Valentine, (1994)] but are related to each other in a hierarchical manner (see also Budd, 1998*b*).

An important question remaining to be resolved, however, is to what extent the functional systems of bilaterians were acquired independently in different lineages – a point that is critical to all assessments of the timing of bilaterian origins.

III. CHARACTER HOMOLOGIES IN BILATERIANS

At the heart of the debate concerning the origins of bilaterians is the problem of character homology between different phyla. If important features such as the blood vascular system, nephridia, segmentation and the coelom are homologous between (for example) deuterostomes and protostomes, then by definition these features were present in their last common ancestor. Conversely, if some or all of these features were acquired independently, then they were not present in the last common ancestor (see e.g. Jacobs *et al.*, 1998 for discussion). As discussed below, these features and their acquisition have crucial implications for the ecology and size of this animal: an animal lacking all of these features would probably be small and perhaps incapable of leaving a trace fossil record, whereas an animal possessing most or all of these features would have almost certainly have been large and a trace-maker (Erwin *et al.*, 1997; Erwin, 1999). This simple view needs careful qualification, because both large, relatively simple animals (sponges and cnidarians) and very small complex ones (members of the meiofauna) exist today. Further, given the current state of uncertainty concerning high-level metazoan phylogeny and characters, it is not possible to offer an instant solution to what is a highly complex problem (see e.g. Jenner & Schram, 1999). Here, we aim to point to some important issues, and to offer a view that is consistent with development and morphology.

The problem of the origins of metazoan phyla is essentially one of phylogenetic reconstruction, i.e. using the known distribution of character states from fossil and especially living animals to infer the states of unknown and unknowable animals, such as the last common ancestor of protostomes and deuterostomes, by a process of character optimization. Demonstrating that a character has a distribution rather than being confined to a single organism is equivalent to demonstrating that the character in question is homologous in the organisms that share it: in other words, homology is regarded as a

synonym of synapomorphy. Modern systematic practice has tended to view the recognition of homology as stemming decisively from the recognition of synapomorphy by character congruence as maximized by parsimony (or some other criterion such as maximum likelihood). Nevertheless, other pre-analysis filters to rule out obviously non-homologous structures must also be applied, leading to the concepts of primary (i.e. pre-analysis) and secondary (i.e. post-analysis) homology (de Pinna, 1991; Hawkins, Hughes & Scotland, 1997). These have included the criteria of *position* and of *special similarity* (Patterson, 1988; Rieppel, 1988; Brower & Schawaroch, 1996). Mere broad physical resemblance has not been generally regarded as sufficient for two features to be entered in an analysis as states of the same character. A classical example of this problem is the coelom. Although many large animals possess a spacious body cavity completely surrounded by mesoderm called a coelom, which in some phylogenetic reconstructions can be seen as a synapomorphy uniting all bilaterians, important developmental differences between different 'coeloms' has raised doubts as to whether these features are actually homologous or are, rather, functional convergences. The difficulty is that because rather few morphological features are available for high-level analysis, each character carries an important burden of the final outcome of the analysis: coding both protostomes and deuterostomes as possessing a coelom is bound to influence heavily the final outcome of the analysis, as would coding the two coeloms separately [see Hawkins *et al.* (1997) for an argument that character states should be seen as aspects of a character, rather than being virtually indistinct from it (Patterson, 1988)]. Nor is testing these distributions against an independent phylogeny such as that provided by molecules of help, because it will not necessarily tell whether or not the two character states in question are independently derived or represent divergences from a single ancestral state. In such a case, it may prove helpful to look at putatively basal organisms to see if any diversity of the character state may be detected in different lineages.

(1) Origin of the coelom: once, twice or many?

The status of the coelom has been the most disputed of all high-level metazoan characters, but it is unfortunately also the most important, because of its functional significance: the presence of a coelom

would almost inevitably imply an organism that could burrow, or was well preadapted to be able to. As argued below, the origin of the coelom cannot significantly predate the start of the trace fossil record (but could postdate it). Pinpointing its phylogenetic origins would thus allow the trace fossil record to be tied into the timing of the origins of major metazoan clades.

Although the coelom, considered as a mesodermally surrounded cavity, has been considered to be homologous in all organisms that possess it, this has now been vigorously disputed. One influential and critical study was that by Clark (1964) who elegantly argued for a separate origin of the coelom in at least protostomes and deuterostomes, giving a functional background to why the coelom must be considered to have been derived twice. Valentine (1994) also suggested on phylogenetic grounds based on ribosomal RNA (rRNA) sequences that at least the deuterostome and protostome coeloms were unlikely to be homologous. The basis for this claim was his placing a 'haemocoel' (which seems to correspond to the 'pseudocoel' of other authors) at the base of the entire protostome clade, including both arthropods and the lophotrochozoans. However, both arthropods and molluscs (and indeed, the other protostomes considered by Valentine, 1994) still possess a coelom, which must in any case precede acquisition of the mixocoelic system of arthropods. Indeed, as implied by Ruppert & Carle (1983), acquisition of the blood vascular system (BVS) must postdate that of the coelom, as blood vessels are constructed from the mesothelia surrounding coelomic spaces. As a result, although animals are known that possess a coelom but not a BVS, the BVS is only found in coelomates (Ruppert & Carle, 1983). Valentine's (1994) ordering of the BVS being gained before a coelom thus seems highly implausible, and there seems no phylogenetic basis from the evidence he presents that protostome and deuterostome coeloms are not homologous.

Classically, coeloms are divided into enterocoels (formed by pouching off the archenteron) and schizocoels (formed by splits within mesodermal clumps of cells lying in the blastocoel). This developmental distinction (not to mention the many different uses that coeloms have been put to) has led to many authors concluding that at least these two types must have been derived independently from one another (Willmer, 1990; Nielsen, 1995; Moore & Willmer, 1997).

This seems an unnecessarily extravagant conclusion. As Bergström (1997) points out, conceptual

simplification of actual developmental modes into one or more simple end-member models may make structures look more different than they actually are. Secondly, demonstration of difference is not proof of separate origins unless one has a typological view of a particular character. Character divergence (and convergence) are to be expected, and homologous states of the same character may be very different from each other. Indeed, the distribution of coelom formation in different groups adds considerable weight to this view of the coelom.

(a) *Deuterostomes*

Although all deuterostomes are meant to be enterocoelous, this is simply not true, unless one takes a view of enterocoely which renders the word virtually meaningless (see Bergström, 1997 for a brief discussion). The mode of coelom formation even within one group is variable, such as the enteropneusts, where up to four distinct types of coelomogenesis have been reported (Hyman, 1959; Nielsen, 1995; Peterson *et al.*, 1999). In general, formation of the anterior coelomic cavity (proto-coel) is enterocoelous, whereas the more posterior mesocoel and metacoel may be formed in a manner closer to schizocoely (i.e. by cavitation of mesodermal blocks that are derived from the endoderm). Similarly, the posterior coelomic cavities associated with the somites of amphioxus may also be considered to be formed by schizocoely (Conklin, 1932). Even some ophiuroids, members of the quintessentially deuterostomous echinoderms, are reported to have a schizocoelous mode of coelomogenesis. Even more complex are the vertebrates, which have a remarkable array of different modes of development, some of which remain poorly known. In teleosts such as the zebrafish *Danio rerio*, for example, no archenteron forms, with gastrulation proceeding by a complex mixture of epiboly, involution and delamination (Kimmel *et al.*, 1995). Endoderm is, if anything, derived from tissues that will generate mesoderm, and the gut is one of the last structures to form. With no archenteron or gut for most of development, there can be no question of enterocoely as a mode of coelom formation. The somites in vertebrates such as the frog are derived from both endo- and ectodermal mesoderm, derived from deep-seated cells within the presumptive ectoderm (but see also below) leading to splanchnic and somatic mesoderm: these then split apart to form the coelom in a manner that is schizocoelous.

(b) *'Protostomes'*

A similar state of variety in coelomogenesis exists within taxa usually regarded as protostomous (and thus archetypically schizocoelous). Although a core of protostomes such as the annelids, molluscs and sipunculans have a 'standard' schizocoelous development, the situation in other groups is not so clear-cut. In the tardigrades, considered to belong to a panarthropodan clade, coelomogenesis has been reported to be by enterocoely (but see Eibye-Jacobsen, 1997 for doubts expressed about the older literature, together with a discussion of the difficulties of studying tardigrade embryology). In the lophophorates, the situation is exceptionally variable, even within a particular genus, and three distinct modes of coelomogenesis have been reported (Chuang, 1991), with *Lingula anatina* demonstrating schizocoely (Yatsu, 1902), and articulate enterocoely (Nielsen, 1991), in an unusual manner similar to that in chaetognaths (Long & Stricker, 1991; Zimmer, 1997). Phoronids, usually considered to be broadly related to the brachiopods, have an extraordinary mode of coelom formation where the anterior 'proto-coel' is formed from migratory amoeboid cells (Zimmer, 1980). Bryozoans also display non-standard coelomogenesis, with for example the stenolaemates forming an initial coelom-like structure as the first stage of gastrulation from presumptive mesoderm (Zimmer, 1997). In the arthropods, the presence of yolky eggs has also often led to a great divergence from anything that could be considered to be 'schizocoely' (Snodgrass, 1935). In insects, for example, the first cells to ingress into the blastula during gastrulation are typically part of the presumptive mesoderm, which can already form paired pouches. The presumptive endoderm is derived from this material, quickly breaking down into lecithophagic cells before the definitive gut finally forms. A snapshot of this development is therefore enterocoelous, although the gut forms after the mesoderm. More difficult to interpret is coelomogenesis in the chaetognaths, the relationships of which have long proved puzzling. Their morphology is broadly 'protostomous', but they have radial, indeterminate cleavage, and form the coelom by folding of the endoderm in a manner that can be considered enterocoelous (Hyman, 1959) and is most similar to that seen in articulate brachiopods and *Crania* (Zimmer, 1997). This mixture of features has led to them being considered deuterostomes, protostomes or basal to both groups, a placement that receives some support from molecular evidence,

Table 1. The logical possibilities for coelom formation based on differences in timing of key events: mesoderm proliferation, coelom appearance and archenteron/gut formation. When coelom formation is early, it appears either as an outpocketing of the gut or even of the ectoderm; when coelom formation is late, it occurs as cavitation (schizocoely) in blocks of already proliferated mesoderm. The six possibilities (A–F) are illustrated in Fig. 4, together with suggestions for examples of each.

Mesoderm proliferation	Coelom first	Coelom second	Coelom third
First	—	Gut third A	Gut second B
Second	Gut third C	—	Gut first D
Third	Gut second E	Gut first F	—

although a broadly protostome affinity may be more likely (Telford & Holland, 1993; Wada & Satoh, 1994; Halanych, 1996).

What does this variability in coelomogenesis imply? The most important conclusion is that variability between modes can occur even in groups that undoubtedly have homologous coeloms – for example, the various hemichordate groups. Contrary to the belief expressed by a recent discussion of the problems posed by the brachiopod coelom that ‘this divergence is inherently unlikely: developmental processes are not so plastic’ (Cohen & Gawthrop, 1997, p. 209) this would indeed suggest that the mode of coelom formation can be and is highly variable. An analogous example is provided by the various modes of gut formation in the vertebrates, which are not generally taken to imply that the guts of various vertebrates are not homologous structures. Indeed, many modes of coelom formation can be made simply by changing the relative timing of the events of gastrulation (considered primarily as archenteron and gut formation), proliferation of presumptive mesoderm and coelom formation (Table 1, Fig. 4), timings that may differ even in different parts of the same organism (such as the enteropneusts). Even mesoderm that is derived from the ectoderm or from the endoderm (or *vice versa*) may thus be placed into the same developmental framework, because especially the ecto-/endoderm distinction is an arbitrary one (particularly early in development): the origin of the mesoderm may again shift by timing changes (i.e. some mesoderm could proliferate early, giving rise to ‘ectodermally’

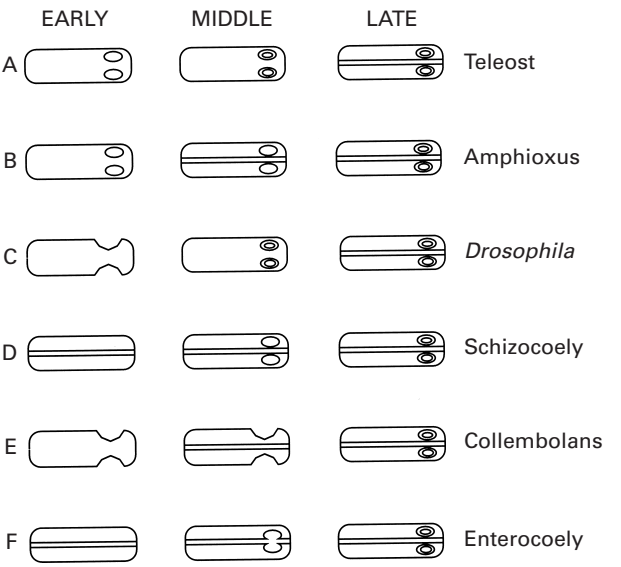


Fig. 4. A conceptual framework for the variability seen in coelom formation, based on timing and rate differences in three processes: archenteron/gut formation; mesodermal proliferation and formation of the coelom itself. By varying the order of these three processes, six possible sequences of events can be generated (see Table 1 for the order of events that letters A–F refer to). As well as schizocoely (D) and enterocoely (F), a variety of other, more difficult to classify modes of coelom formation may be incorporated into the same scheme, strongly suggesting homology between the modes. Some suggestions are given on the right of the diagram for examples of each mode of formation. See text and Table 1 for further details.

derived tissues; other mesoderm could proliferate late, giving rise to ‘endodermally’ derived tissues, depending on how gastrulation has progressed). Part of the difficulty in distinguishing germ layers in early development has been recognized by authors referring to the mesendoderm for example, which in teleosts and some insects eventually gives rise to both mesoderm and endoderm.

Different modes of coelom formation may thus all be seen to lie in a continuum governed by relatively trivial differences in timing. They do not give support to the idea that the various coeloms must be derived independently in different organisms, and in the absence of the all-important phylogenetic evidence to the contrary (e.g. the demonstration of a highly paraphyletic ‘flatworm’ grouping at the base of the bilaterians) the working hypothesis must be that coeloms are in general homologous structures. The logical, but unpalatable, alternative to this conclusion is that even amongst very closely related organisms such as a single genus of brachiopods, the coelom must have been independently derived on

multiple occasions, even when morphologically virtually identical. It should be noted that although some classifications (e.g. that of Willmer, 1990) have indeed placed a flatworm-like organism at the root of the bilaterian divergence, this has been on the assumption that the various coeloms are not homologous – but this is the wrong way round to proceed.

(2) Character loss and gain: optimizing in a complex tree

The above arguments are important for establishing character homologies in ancestral organisms. In general, the demonstration of homoplasy is an empirical question, and the very possibility of being able to list impressive homoplasies (Moore & Willmer, 1997) tells us that there are empirical methods of detecting them. Merely to suggest that two similar structures might be homoplastic without any supporting empirical evidence is thus empty. This empirical evidence comes partly from morphological analysis, but the more remarkable the convergence, the more difficult it becomes to rely on such a method, and for reasons given above, this may mistake divergence for convergence. The primary reason for regarding two structures as homoplasies must thus be phylogenetic. For example, arguments concerning whether marsupial and mammalian carnivores have homologous sabre-teeth (Conway Morris, 1998*c*) rest almost entirely on our knowledge of the phylogeny of the two groups, not on details of tooth structure. We wish to separate out here the slightly different question of contingency, which is connected with convergence (Conway Morris, 1998*c*). One may hold to the view that mechanico-physical constraints on animal evolution would imply that ‘re-run’ evolution would give rise to similar results to those we see today (*contra* Gould, 1989; see Conway Morris, 1998*c*) whilst still empirically considering that the actual features we see in extant taxa are in general homologous. One might thus argue that if evolution was re-run, one would expect to see the same set of structures evolve monophyletically.

Nevertheless, no matter how similar characters like the coelom appear from one organism to the next, homoplasy might still need to be inferred if one coelomate branch or another possessed a series of basal, non-coelomate plesions. This could be interpreted either as suggesting that the coelom was not present (or was lost) in the stem of that clade, and was subsequently (re)gained; or that the plesions have themselves each lost the coelom, an option that

might not be the most parsimonious. Indeed, strictly considered, the profound question of whether the coelom was homologous or not between the deuterostomes and protostomes might hinge on the placing of one minor phylum (see Fig. 5). Nevertheless, this assumption of exact equivalence between the two character transformations (coelom loss and coelom gain) runs contrary to the intuition that complex character states (e.g. possessing a coelom) are more ‘difficult’ to acquire twice than are simple character states (e.g. not possessing a coelom). There is no reason why the phylogenetic ‘cost’ of each of these transformations should be exactly identical in reality, even if phylogenetic methods in general treat them as such. A recent attempt to use a tree itself to assess the relative ease of these sorts of complementary transformations, and then apply that weighting to the entire tree to recalculate the most parsimonious character optimization based on the new weighting, has been made by Goloboff (1997). He gives the example of winged and wingless insects: the presence of thoracic wings allow one to assign an arthropod to the pterygotes with some certainty, but the absence of wings does not so easily allow one to classify the arthropod with any other group of organisms, or even as a ‘non-pterygote’, because of the presence of many clades of wingless ‘pterygotes’, such as wingless grasshoppers, mantids, stick insects and so on. Given what is known of insect relationships, it seems that possessing wings is a far more reliable character when considered as a potential homology than that of not possessing wings. In the case of the coelom, or of other characters possessed by large clades of bilaterians, many cases of secondary loss of such characters are reliably now known (see Hanken & Wade, 1993 for review), but very few examples of homoplastic gain. For example, within the annelids, it is likely the coelom has been lost several times in the ‘archannelids’ [now widely seen as a polyphyletic assemblage (Westheide, 1985)], segmentation has been lost in the echiurans, and the gut has been lost in the pogonophorans (McHugh, 1997). In the arthropods *s.l.*, many ‘body-plan’ features can be reliably be documented to have been lost in taxa such as the pentastomids, rhizocephalans and tardigrades. In the molluscs, even more extreme cases are known, such as that of *Xenoturbella*, which in some accounts is a highly derived bivalve (Israelsson, 1997; 1999) – in this case, so many morphological features have been lost that it is only recently that its molluscan and bivalvian affinities have been recognized at all. In contrast, convincing documentation of secondary

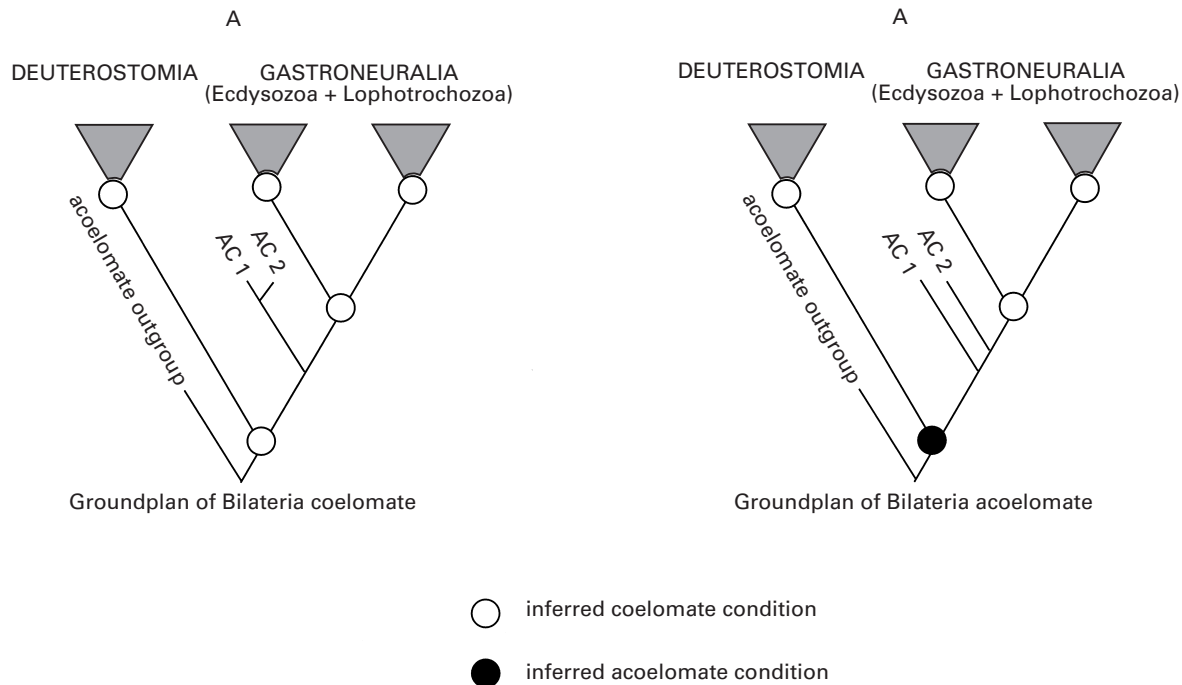


Fig. 5. Character optimization in complex trees. If the assumption is made that the phylogenetic 'cost' of character reversal is the same as character gain, then character optimization and subsequent identification of homology may be highly unstable. In (A), all major bilaterian clades are recognised to have a coelomate groundplan, and a coelom can be inferred to be present at the base of the Bilateria too. In (B), however, the position of two minor acoelomate phyla (AC1 and AC2) as successive plesions to (e.g.) the Gastroneuralia, rather than forming a clade of their own as in (A), forces non-homology of the coelom across all the Bilateria, and thus suggests an acoelomate groundplan overall. Major character homologies might thus be dependent on the systematic position of small acoelomate groups.

gain of complex structures within clades of 'simple' organisms is surprisingly lacking. Hypothetical examples might include taxa within the acoels or other flatworms with a coelom or BVS. One potential exception to this generality is perhaps provided by the BVS of the nemerteans, although it is interesting to note in this case that this feature is clearly very different from the classical BVS of other bilaterians (Ruppert & Carle, 1983). In any case, this structure may be homologous to the coelom of other protostomes, so it represents functional shift rather than secondary gain. The presence of one or more pores connecting the gut diverticulae in some flatworms to the outside should be considered a convergence with the mouth-anus system of other bilaterians (Ehlers, 1985), and given that this arrangement does not approach the through-gut system, it has generally never been thought to be homologous with it. As one more example, the segmented nemertean *Annuloneurtes* has been suggested to be a possibly secondarily segmented organism (Berg, 1985). However, as Berg (1985) discusses, if the nemerteans are placed within the context of a segmented protostome clade rather than a non-segmented acoelomate one

(Turbeville, Field & Raff, 1992), then its segmentation may be a retained plesiomorphy rather than a derived autapomorphy.

The known phylogenetic examples are thus strongly in favour of the intuition that complex body-plan features are indeed more easily lost than gained. If such information were to be applied to an overall cladogram of the bilaterians, then the possibility of the major features such as segmentation, the coelom, metanephridia etc. plotting as homologies would no doubt be greatly enhanced [see Jacobs *et al.*, (1998) for such an attempt for two features, eyes and the heart. They conclude that phylogeny does not support heart homology. However, their analysis relies on Hyman's (1959) view of phylogeny, which may be being superseded, and does not take into account the arguments of Goloboff (1997) presented above].

IV. IS THERE AN EXTENSIVE PRECAMBRIAN HISTORY OF METAZOANS?

Whatever the order of appearance in the fossil record of the phyla is, the possibility of a considerable but

cryptic Precambrian metazoan history has proved to be an attractive one. Two issues arise: first, is there fossil evidence for an early origin of bilaterians, and secondly, can the known fossil record be reconciled with any of the current theories that propose early origins?

(1) The early fossil record of animals

The Proterozoic bilaterian fossil record may be sought in the Ediacaran biota (Glaessner, 1984; Gehling, 1991; Fedonkin, 1992; Runnegar, 1995; Narbonne, 1998). No current consensus exists about the biological affinities and degree of heterogeneity of these assemblages. However, one emerging point of agreement is that the Ediacaran organisms should not be 'shoe-horned' into one taxonomic category (Runnegar, 1995; Seilacher, 1999), even at a high level. The purpose here is to review briefly whether the roots of the Phanerozoic bilaterian fauna may be detected in the Ediacaran assemblages.

A major complicating factor is that the typical preservation of the fossils of the Ediacaran biota as casts and moulds on surfaces of relatively coarse sediment inevitably results in considerable loss of detail. Some forms with a modular construction, notably *Ernietta*, *Phyllozoon* and *Pteridinium* cannot even reasonably be considered to have metazoan affinities (Runnegar, 1995; see Dzik, 1999 for a radical alternative bilaterian interpretation of *Ernietta*). The common disc-shaped forms such as *Cyclomedusa*, many or all of which may have been basal holdfasts of fronds, are likely to have cnidarian affinities. A number of Ediacaran fossils have been compared with annelids and arthropods [(e.g. *Spriggina*, *Parvancorina* and *Dickinsonia* (Glaessner, 1984)]. One of the classic Ediacaran taxa, *Dickinsonia*, consists of numerous narrow 'segments' with an anterior-posterior polarity. Jenkins (1996) and others claim that other details such as notopodial elytra and a pharangeal region, paired gastric caecae and filled intestine are preserved. However, none of these are generally accepted to be present, and have yet to be convincingly documented. Probable evidence of musculature contraction suggests, but does not demonstrate, eumetazoan affinity (Runnegar, 1995). At present though, no clear evidence to link any of these taxa to the Bilateria exists. Other taxa that have been suggested to be cephalized and segmented include *Parvancorina* and *Praecambridium*. Frequent comparisons have been made with trilobite protaspids (Glaessner & Wade, 1971; Fortey *et al.*, 1996). However, at present this similarity stands

in need of detailed comparative study, and does not currently convince (Hou & Bergström, 1997). Waggoner (1996) attempted to resolve the issue of the affinities of these forms with a cladistic analysis, which grouped many of them close to the arthropods. The validity of such an approach, however, depends on initial character state assignment, which in this case is controversial (Budd, 1999b).

Perhaps the strongest case for an Ediacaran bilaterian body fossil has been made by Fedonkin & Wagonner (1997) for *Kimberella*, which they describe as mollusc-like. It is a relatively large, bilaterally symmetrical organism, which they reconstruct as possessing both a dorsal shell and a 'foot'. Nevertheless, *Kimberella* does not possess any unequivocal derived molluscan features, and its assignment to the Mollusca or even the Bilateria must be considered to be unproven (cf. Erwin, 1999).

A prominent group of Ediacaran organisms were conical with tri-radial symmetry, such as *Tribrachidium*, *Albumares* and *Anafesta*. Although these have been compared to echinoderms, they again lack convincing synapomorphies, and can as easily be seen as cnidarians (Fedonkin, 1990) or even poriferans (Seilacher, 1999).

This cursory review of Ediacaran forms suggests that there are some reasonable candidate bilaterians, but that these so far defy closer comparison with Phanerozoic groups. Terminal Proterozoic phosphorites in south China have yielded structures purported to be animal embryos of probable bilaterian affinity (Xiao, Zhang & Knoll, 1998). However, these structures clearly demand further analysis, to confirm both their metazoan and bilaterian affinities. The strongest evidence for Ediacaran bilaterians comes rather from the trace fossil record, although here too considerable caution must be exercised.

(2) Terminal Proterozoic trace fossils

The first uncontroversial animal trace fossils post-date the last stage of Proterozoic glaciations (Marinoan or Varanger Ice age), which ended around 590–570 Ma (Knoll, 1996) or perhaps even later (Saylor *et al.*, 1998). There are numerous reports of older trace fossils, but most can be immediately shown to represent either inorganic sedimentary structures, or metaphytes, or alternatively they have been misdated. Indeed, no pre-Marinoan putative trace fossils stand up to critical analysis (Crimes, 1994; Fedonkin & Runnegar, 1992). A recently reported 1 billion years ago (Ga)

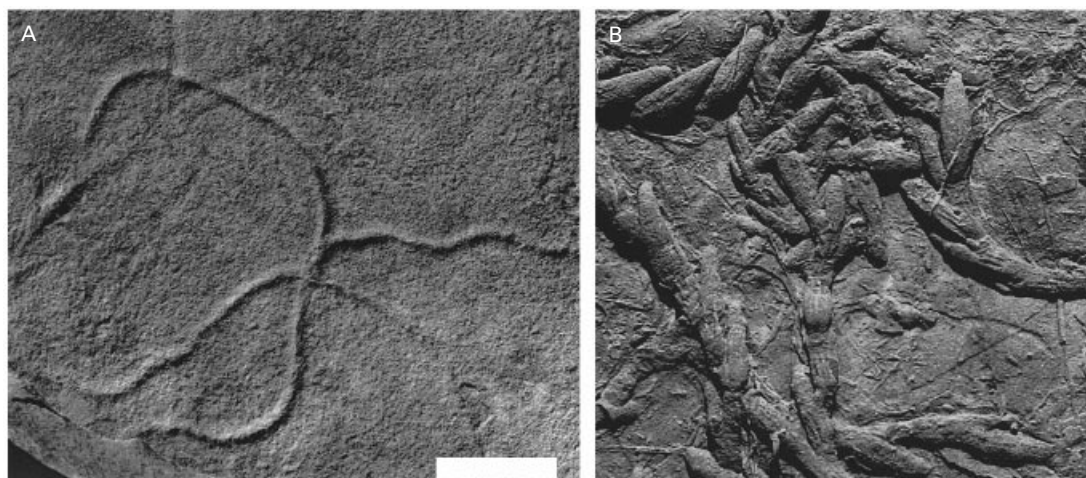


Fig. 6. (A) *Helminthoidichnites*, irregularly meandering terminal Proterozoic trace fossils from the Rawnsley Quartzite, South Australia, preserved as a groove on the upper surface of a parting lineation. This horizontal trace was made close to the sediment surface. Scale bar, 5 mm. (B) *Treptichnus pedum*, complex branching trace fossils preserved at the base of a sandstone bed, Sellick Hill Formation, South Australia. This type of trace fossil is characteristic of Cambrian sediments, but more simple forms also rarely occur in the terminal Proterozoic. Scale bar, 5 mm.

trace from India (Seilacher, Bose & Pflüger, 1998) can be regarded as probably inorganic because of the gradually tapering pointed terminations and variations in width within a single 'trace'. Additionally, the irregular 'crinkly' development (see Fig. 3 in Seilacher, Bose & Pflüger, 1998) is more like that of tensional cracking. This analysis stands whether or not the host sediments are correctly dated (Brasier, 1998). An approximately 600 Ma trace from Scotland identified as a chain of ovate pellets (Brasier & McIlroy, 1998) is also dubious because of its poor preservation. Terminal Proterozoic trace fossils are generally simple and essentially horizontal, and were constructed close to the sediment surface (Crimes, 1987; Fedonkin & Runnegar, 1992; Fig. 6). There is an increase in complexity, three-dimensional exploitation of the sediment and diversity of trace fossils immediately before the Cambrian (Jensen *et al.*, 1999, in press; Fig. 7). This increase continues into the earliest Cambrian (Nemakit-Daldynian), with a further increase in the Tommotian (Narbonne *et al.*, 1987; Fedonkin & Runnegar, 1992; Crimes, 1987, 1994). With the recent re-evaluation of several 'complex' terminal Proterozoic trace fossils as having other origins, the picture is that of a steady increase in diversity and complexity.

The presence of latest Proterozoic trace fossils raises the question of the trace-makers. The supposed presence of rows of fecal-pellets has been seen as evidence of animals with a through gut, which in principle implies a bilaterian form. However, these traces are among those currently being re-evaluated

(Jensen *et al.*, 1999). Although simple horizontal traces are conventionally assigned to bilaterians, certain cnidarians are also capable of producing surprisingly complex traces. These include burrowing sea anemones (Jensen, 1992). Indeed, there are globular Ediacaran fossils at the end of what appear to be a meniscate trace perhaps formed during lateral movement (Fedonkin, 1983). Nevertheless, the majority of terminal Proterozoic trace fossils are burrows with morphological features or patterns of movements such as meanders and spirals which are consistent only with a bilaterian *s.l.* producer. In particular, the presence of simple treptichnids (Jensen *et al.*, in press), strongly suggests a degree of complexity beyond that known to be attainable by cnidarians. Another possible line of evidence comes from marks resembling radula-type imprints found in the terminal Proterozoic of Australia and the White Sea (Seilacher, 1997), but these await detailed description.

The combined evidence of the trace and body fossils from the terminal Proterozoic, then, suggests that convincing crown-group bilaterian body fossils are not known before the Cambrian, and trace fossils that may be reasonably attributed to at least stem-group bilaterians are known from approximately 550 Ma, which show an increase in complexity up into the Cambrian. Despite this important negative evidence, the notion of metazoans having evolved well before this time has been suggested on several grounds: first that the apparent sudden appearance of the modern phyla at the base of the Cambrian

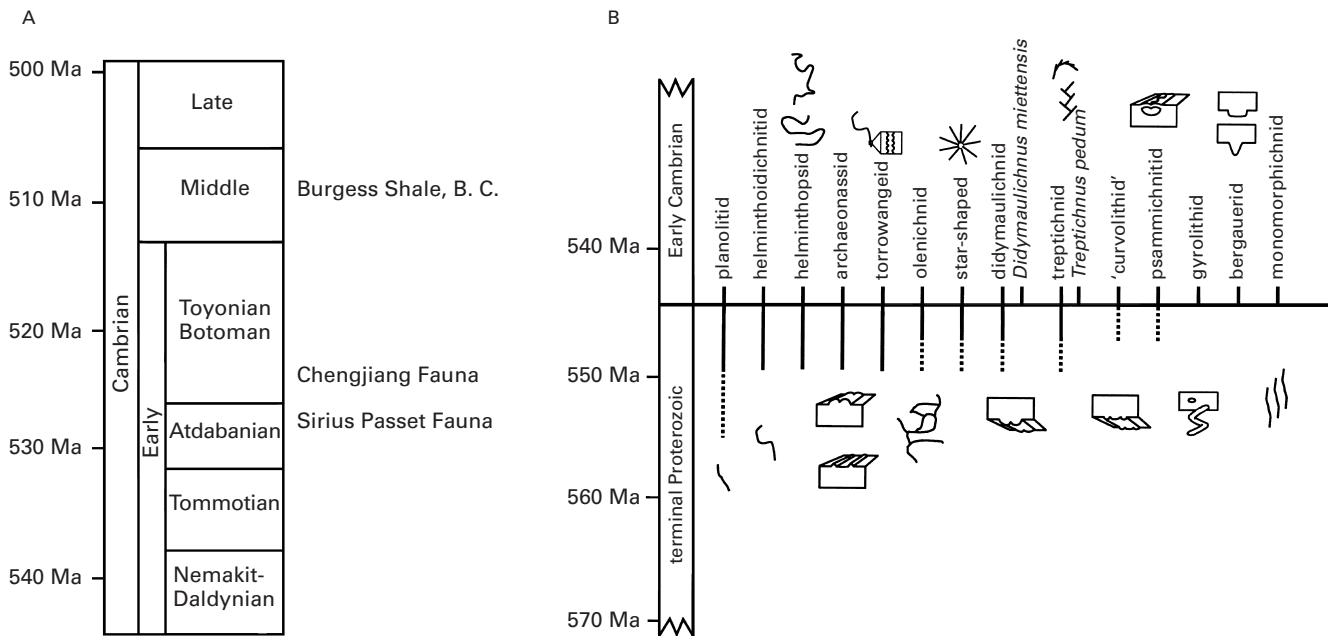


Fig. 7. (A) Composite time scale and stratigraphic sequence of the Cambrian, together with the approximate levels of the three major exceptionally preserved biotas. Dates based loosely on Tucker & McKerrow (1995). It should be noted that a widely divergent array of dates and correlation for the Cambrian have been published (cf. Davidek *et al.*, 1998; Landing *et al.*, 1998). (B) A preliminary scheme for the stratigraphic appearance of the major types of terminal Proterozoic trace fossils, here grouped under broad morphological headings. Compiled from the literature and work in progress. In this new scheme, there is no terminal Proterozoic disappearance ('extinction') of ichnogenera, but rather a successive appearance of more complex trace fossil morphologies.

virtually demands some sort of Precambrian history (Fortey *et al.*, 1996); and secondly that on the grounds of 'molecular clock' data, the time of metazoan divergence may be at least 1 Ga (Runnegar, 1982a; Wray, Levinton & Shapiro, 1996; Bromham *et al.*, 1998; Cooper & Fortey, 1998; Wang, Kumar & Blair Hedges, 1999; but see also Ayala & Rzhetsky, 1998; Conway Morris, 1997, 1998a; Lynch, 1999 for more moderate views). For example, in a recent review (Knoll & Carroll, 1999) the staged appearance of phyla in the Cambrian is noted, but because these are regarded as crown-group taxa, stem-group divergence is still postulated to have occurred in the Proterozoic. The lack of convincing metazoan fossil evidence for this period has been explained in the following ways:

(i) That ancestral metazoans were tiny (possibly meiofaunal) and the Cambrian explosion represents a sudden size increase in many lineages (Cooper & Fortey, 1998; Fortey *et al.*, 1996; Fortey, Briggs & Wills, 1997). In support of this view, it has been suggested that the sister-groups to many phyla are tiny (e.g. the tardigrades for the arthropods, aplousobranchs for molluscs and pterobranchs for deuterostomes), together with the view that the fossil record of sudden appearance cannot be read literally

because key taxa such as the trilobites appear suddenly with a standing diversity and established biogeography, implying some cryptic history (Fortey & Owens, 1990).

(ii) That ancestral metazoans were planktonic and relatively simple, and that phylum-level features arose suddenly near the base of the Cambrian (Davidson *et al.*, 1995; Peterson, Cameron & Davidson, 1997). This view is supported by notions of indirect development playing a crucial role in metazoan evolution (Jägersten, 1972; Nielsen, 1995), with the ancestral larvae-animals developing 'set-aside' cells with a decoupled developmental program that would go on to develop into benthic adults. In support of this hypothesis is offered the widespread distribution of maximum indirect development in marine phyla, the alleged rapid appearance of the phyla at the base of the Cambrian, the apparent lack of homologous features uniting the extant phyla, and the description of the sort of division of developmental mechanisms that is required by the theory.

(iii) That some stem-lineage metazoans arose early and were large animals, but have not been discovered simply because of their rarity and/or cryptic habitat (Balavoine & Adoutte, 1998;

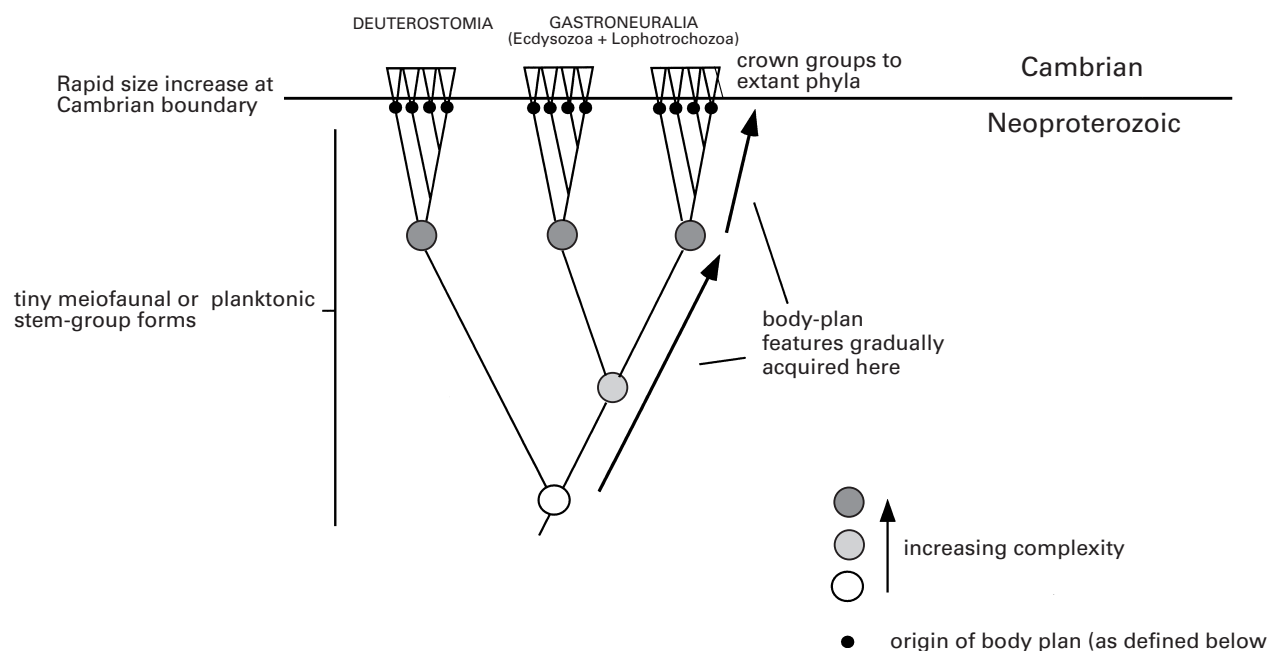


Fig. 8. The scenario for early bilaterian appearances of Fortey *et al.* (1996, 1997). Bilaterian ancestors emerge deep in the Proterozoic but are tiny, possibly planktonic or meiofaunal. Their subsequent appearance in the Cambrian fossil record is a reflection of rapid body size increase, perhaps as the result of an increase in oxygen level rise at this time.

Adoutte *et al.*, 1999) This view has been supported by the claim that small animals are scattered through clades consisting of larger animals rather than comprising sister-groups to them.

We aim to demonstrate below that these scenarios, and indeed all scenarios involving an extensive but cryptic Proterozoic history of bilaterians, may have strong objections lodged against them. We have selected these particular models for discussion because of their recent prominence and the introduction they provide into the many complex and interesting issues involved; it is not our intention to single them out for particular criticism, although as discussed below, our views diverge markedly from these authors.

(3) Missing stem groups in the Proterozoic?

In the scenario of Fortey *et al.* (1996, 1997) (Fig. 8), some of the very evidence urged for the scenario (the evidence from trilobites – see Fortey & Owens, 1990) may actually count against it. Trilobites may appear abruptly: but the last common ancestor to polymerid trilobites such as the olenellids and redlichids [which make up the major biogeographic groupings in the Early Cambrian (Lieberman, 1998; but see Lieberman, 1999 for some doubt cast on the validity of these groupings)] was undoubtedly a large animal

with a calcareous exoskeleton with high preservational potential. Its absence from the fossil record cannot be explained on the grounds that it was either meiofaunal or non-calcareous, and it is likely that there is thus a genuine – but probably short – gap in the trilobite fossil record at this point. Rather than pointing to an extensive cryptic prehistory of metazoans, the evidence from the trilobites seems to count for a cryptic period of history (for at least one lineage) – a crucial difference, because the demonstrable lack of record cannot be generalised to explain the lack of fossils in the Proterozoic (whereas non-appearance in the earliest Cambrian because of low preservation potential could be). Other ancestral metazoans could conceivably be hiding in this as yet poorly understood period of earth history. Whilst Fortey *et al.* (1997) therefore seem correct to stress that some metazoan evolution is not accounted for by the known Cambrian record, there seems no reason to postulate an enormous cryptic history.

The suggestion that the distribution of small animals implies small size was an ancestral bilaterian feature seems not sufficiently supported: mere demonstration of a small animal as a sister-group to a clade of larger animals is not enough to establish small size as primitive. What is really required is to be able to reconstruct character states at internal nodes in a cladogram, and a series of plesions of small animals would be required to demonstrate small size

as being ancestral to a clade. As an example, the tardigrades may be the sister group to the arthropods, but the large onychophorans are the sister group to tardigrades + arthropods. Consideration of the fossil record suggests that arthropods may in fact have evolved from within a paraphyletic assemblage of unusually large animals (Budd, 1997, 1998a), and that the tardigrades are secondarily miniaturized (but see also Schmidt-Rhaesa *et al.*, 1998). This difficulty applies equally well to the argument given to opposite effect by Balavoine & Adoutte (1998, see below): distribution of taxa is not as important as the inferences that can be drawn about internal character states from them. The other argument (Fortey *et al.*, 1996, 1997) – the sudden appearance of phyla in the Cambrian requires an extensive prehistory – requires modification in the light of arguments given above: despite extensive cladogenesis, the modern phyla *s.s.* in general evolved after the beginning of the Cambrian. Such a view is supported by modelling of cell type number increase throughout the Phanerozoic (Valentine, Collins & Meyer, 1994). This implies that the Cambrian was typified by the creation of ‘new morphogenetic patterns rather than the wholesale evolution of major new levels of tissue and organ complexity’. Potentially, an extensive Precambrian history of phyla may be removed by postulating an extensive Phanerozoic history of phyla origination and increase in complexity instead.

(a) *System evolution and functional thresholds*

A more serious argument against the view of Fortey *et al.* (1996, 1997) is that it fails to take into account the functional aspects of metazoan structure and evolution. Whilst it is true that there are many tiny metazoans today (less than 1 mm in length), it does not necessarily follow that bilaterians as a whole did or indeed could have evolved in a meiofaunal setting (as in the scenario proposed by Boaden, 1989). An analogy is provided by sea-going mammals and reptiles today such as whales and turtles. Their presence in marine settings is undoubted – but does this imply that features such as fur, the mammalian jaw, hearing apparatus and distinctive skeletal structure could have evolved in such a setting – even if they are in some cases retained there? Proponents of a ‘correlated progression’ view of evolution that see evolution of form as being indispensably linked to ecology and function (Kemp, 1982, 1985, 1988; Lee & Doughty, 1997) would decisively reject such a view (see also Edlinger, 1998 for a useful discussion

of the phylogenetic implications of constructional morphology). In an insightful paper, Jaanusson (1981) argued that functionality could not be necessarily smoothly transferred from one biologically complex system to another in evolution. This argument might be recast as follows: as a biological system evolves, the selective pressures acting on it might not always act to change the system from one functional type to another, even if the target system would be advantageous to achieve (Edlinger, 1991; Edlinger & Gutmann, 1997). It is therefore not sufficient to line up a series of morphological intermediates from one system to another to demonstrate that an evolutionary transition could have occurred: a continuously favourable functional improvement in the relevant environments must also be demonstrated, showing that the functional threshold can be overcome in certain, perhaps restricted ecological settings (a point that Jaanusson, 1981 neglects). The concept of a functional threshold is of particular relevance when considering postulated large increases in size. Not only does the nature of the physical environment change dramatically with size, as Reynolds number changes (governing the relative effects of inertial forces and viscosity), but many other processes such as diffusion also take on a radically different character (see e.g. Hanken & Wake, 1993 for a review and references, especially for vertebrates). For example, in a tiny animal, cilia action is sufficient for motion, and no muscle, body cavity, complex nephridia or blood vascular system is required (e.g. Sleight & Blake, 1977; LaBarbera & Vogel, 1982; Ruppert & Smith, 1988). As such an animal is hypothetically enlarged, its small-scale systems will remain appropriate up to a certain body size, beyond which their functionality will decline, and this will act as a natural limit on the size that animals organized in such a way can attain (Fig. 9). For a system appropriate to large size, such as a blood vascular system, to evolve in a tiny animal, one must ask the critical question, not just whether this system would in fact be advantageous in the small animal, but whether or not it could be assembled in the small animal.

The mere existence of tiny metazoans today, some of which retain systems appropriate to large animals (although loss seems to be far more common), is therefore not of relevance to the question of how such systems were initially assembled. Although this argument is thus superficially like the ‘what use is 5% of an eye?’ argument, in reality it deals with a different issue, the eye analogy to which would be to

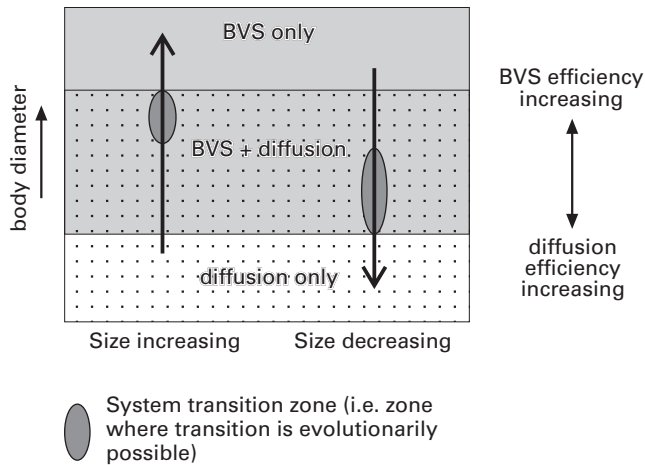


Fig. 9. Character gain and loss during size change, indicating the 'hysteresis' involved: size change in one direction does not necessarily result in the same sequence of events as size change in the other direction. Here, the blood vascular system (BVS) is taken as an example. Two fields are marked: where a BVS is functionally possible, and where diffusion is functionally possible: the two together define a third region where either may be used. Functionality of each system is likely to decrease significantly as the limits of the respective fields are reached. A small animal increasing in size may not be able to develop a BVS either directly or preadaptively until the evolutionary cost of building it is outweighed by the advantages of possessing it, thus overcoming the 'functional threshold' of Jaanusson (1981), i.e. at the base of the 'transition zone' marked. Conversely, a large animal decreasing in size may retain a BVS for longer, although the transition zone here might be longer: depending on other systems associated with it, the BVS may be lost at larger sizes than it would be gained. The lack of a BVS (or functional equivalent) in relatively long animals such as *Xenoturbella* suggests that the BVS may not be necessary in organisms shorter than centimetre size (although even in this organism the tissue thickness remains small); the lack of a BVS in animals smaller than approximately 3 mm suggests that the lower limit is around this size (cf. LaBarbera & Vogel, 1982; Vannier & Abe, 1995). An example of this sort of change is provided by flatworms, which as they increase in size do not immediately develop a BVS, complex musculature etc, but rather become flatter and thereby manage to retain their ancestral systems (Clark, 1964). Oxygen levels may affect maximum and minimum body size with respect to the BVS and other transport or diffusion systems, but not with respect to muscle, which depends on biomechanical constraints. The mere presence of complex systems in small metazoans does not thereby imply that they could have evolved at such sizes.

ask whether or not a proto-eye could evolve in an animal that lived in total darkness. Although this possibility cannot be ruled out for every system

(indeed, preadaptation is essential to the problem of bridging functional thresholds), for the case of the eye and the blood vascular system, such a scenario seems extremely unlikely. Clearly, just as a proto-eye in a light-deprived organism could not have evolved for any purpose of vision, the BVS could not have evolved as a system for transporting blood around a tiny body. If such a structure were to evolve in a small animal, one might wish to ask what purpose it in fact played. The structure of the BVS – a set of more or less enclosed tubes that are distributed in every part of the body – strongly suggests that the system arose for some sort of communication or transport, even if not of blood. However, the tiny size of the organism rules out the need for any such transport structure. In effect, the constructional morphology of the BVS virtually rules out the possibility of it having evolved for any purpose in a tiny animal. This, in turn, suggests that the BVS first evolved in a larger animal. The implications for the invertebrate phyla are clear. Large animals (such as polychaetes and crustaceans) in general possess a structural apparatus that is closely linked with their particular environmental challenges. Body cavities, blood vascular systems, complex muscular and support systems, and nephridia (or – critically – some sort of functional equivalents) are all features that are required in large animals, but not in tiny ones, where ciliated soles may suffice for movement, and diffusion for excretion and respiration. If the ancestral bilaterian was itself small (but see below), then some of these features may have evolved preadaptively in a small animal. Indeed, a central challenge facing palaeontologists and functional morphologists is the analysis of what pattern of preadaptation and co-option characterizes metazoan evolution (see Budd, 1998*a*; Ganfornina & Sanchez, 1999 for morphological and molecular examples respectively). Nevertheless, the appearance of the integrated complex or syndrome of features mentioned above in a very small animal is highly implausible, just as although some aspects of the tetrapod limb may have evolved preadaptively in a fresh-water setting, the sum of tetrapod features surely did not. Thus, in so far as body plan features of the extant phyla represent homologies across the Bilateria (and, as argued above, hardly any empirical evidence has been presented to the contrary), the animal in which they evolved would have been moderately large, a critically important point when considering the importance of the trace fossil record (see below).

One obvious question raised by this analysis is the

limits placed on system functionality in different settings: when does an animal count as 'small' or 'large' for these purposes? Much work remains to be carried out on the effect of size change on system functionality in invertebrates (e.g. Edlinger, 1998; Ruppert & Smith, 1988), following the pioneering work of Clark (1964), and the answer to this question is not as yet entirely clear. Nevertheless, Clark's (1964) review of locomotion in flatworms suggesting that the transition between ciliated and muscular creeping would take place in animals somewhat over 1 mm in length is significant (Sleigh and Blake, 1977); the latter authors suggest that the lower limit for muscle action is in organisms approximately 0.1 mm long. Westheide (1997) suggests that the animal giving rise to the annelids was considerably larger than this, although the basis for his assessment is not clear. For the BVS, calculation and observation on extant ostracods (Vannier & Abe, 1995) suggest that the largest ostracods without a BVS are not much more than 3 mm long, and all ostracods below this limit lack a BVS, suggesting that organ systems are not generally retained in tiny animals. In extremely small animals, the question of space also becomes significant. Animal cells must be a certain size in order to accommodate the cellular apparatus such as (most importantly) the nucleus, mitochondria, endoplasmic reticulum and Golgi body. At tiny sizes, the size of cells relative to the structures being constructed out of them becomes significant. Multi-layered, complex construction thus becomes increasingly difficult at smaller and smaller sizes. Secondly, the relatively large size of the constituent cells compared to the body means that the body becomes increasingly rigid (Edlinger, 1998), implying that movement must rely on ciliary motion rather than muscular contraction and a hydrostatic coelom. The minimum size of complex animals is therefore definitely limited, and it is significant that although some small animals retain complex systems, the tiniest metazoans (such as some rotifers and acoel flatworms) invariably have highly reduced organ systems, including lack of a coelom. On constructional grounds then, the oldest bilaterians must have been relatively large animals. The effect of oxygen concentration on these arguments is also important to consider though, and is discussed further below.

(b) *Trace fossils and functional morphology*

From the above discussion, one may conclude that key features of early bilaterians developed in rela-

tively large animals, a point, incidentally, supported by out-group analysis – both cnidarians and sponges are relatively large (cf. Rieger, Haszprunar & Schuchert, 1991; Rieger, 1994 who strongly question the traditional view of ancestral bilaterians being tiny). However, the functional backdrop to such developments is unclear. To take the example of the annelids: Clark (1964) proposed that the segmented coelom arose as a response to burrowing (and thus suggested that oligochaetes were primitive relative to polychaetes). However, this view has not been generally supported, and more recent suggestions (backed up by phylogenetic analysis) are that polychaetes are primitive. In this scenario, the segmented coelom arose for improving the efficiency of surface locomotion (Conway Morris & Peel, 1995; Westheide, 1997). The timing of such a development need not necessarily be constrained by the trace fossil record, because walking traces are typically not preserved in the fossil record, unless they create an undertrack (Goldring & Seilacher, 1971). One might conclude from this that the earliest bilaterians could considerably predate the first trace fossils, because they may not have been burrowing organisms. Few, if any traces formed near the sediment/water interface in marine settings are likely to enter the fossil record: they are likely to be destroyed by bioturbation or physical disruption (Bromley, 1996; Hertweck, 1972). This surficial mixed layer may be recognized in vertical sections as an ichnofabric. A comparative study of terminal Proterozoic and Cambrian ichnofabrics in South Australia demonstrated that despite the presence of discrete trace fossils in this layer, the terminal Proterozoic ichnofabric was negligible (Droser, Gehling & Jensen, 1999). The presence of these traces suggests that near-surface activity could indeed be preserved in the Proterozoic, and the view that the traces of early bilaterians would not have been preserved may thus be seen to be unlikely, for the following reasons.

(i) The Proterozoic may have provided particularly favourable conditions for preservation of surface and shallow traces. Preservability of trace fossils depends on both the type of activity represented by the trace, and its sedimentary context (Bromley, 1996). In an homogeneous sediment, the trace fossils with the highest preservation potential are permanent dwelling structures: traces made by movement through the sediment are less likely to be readily recognized unless enhanced by diagenesis, as the newly made trace will be quickly refilled with a non-contrasting sediment. Traces recording infaunal vagile behaviour preserve especially well where sand

and silt overlies a finer sediment, as traces in the mud act as moulds for the overlying sand to cast or be piped down into. Such a sedimentary setting is provided, for example, by sand- or silt-rich storm beds being deposited in areas of normal mud deposition. Thin storm-beds in particular would have a good survival record in the absence of intensive bioturbation (Sepkoski, Bambach & Droser, 1991), i.e. in the conditions of the Proterozoic. Conditions for the preservation of infaunal activity would therefore seem to have been enhanced in the Proterozoic where it occurred. Such arguments also apply to the preservation of surficial traces, especially when the essentially arbitrary distinction between epifaunal and infaunal activity is taken into account. An animal crawling over fine sand may create a trace by pushing sediment to either side, as seen in modern gastropods. A surface trace on a non-cohesive sand surface could readily be preserved by being buried with even a thin veneer of suspended mud from a distant storm event, because any bioturbation subsequent to this would be confined to the top-most layers of sediment.

It has been suggested that primitive locomotory organs, for example the broad ciliated foot of many molluscs, developed for movement over hard substrates, and would thus not be recorded in the fossil record. However, a study of rocky shore gastropods, showed that this form of locomotion, using a combination of ciliary movement and muscular contraction, also permits movement over soft substrates (Truemann & Brown, 1993). Again, such shallow traces would, as discussed above, have had greater preservation potential in the Proterozoic.

To summarize, neither shallowness of traces nor substrate preference seem to exclude the possibility of trace fossil preservation in the Proterozoic.

Secondly, binding of non-cohesive sediments by microbial and algal mats increases their resistance to disruption and erosion by currents (Paterson, 1994). This is significant in the light of strong indirect evidence that clastic sediments in the terminal Proterozoic were indeed often bound by such mats to a much greater degree than today (Pflüger & Gresse, 1996; Gehling, 1999; Hagadorn & Bottjer, 1999). Traces formed on a newly-deposited sand layer would therefore have been protected by a mat from the next phase of sediments or currents. Thus, although the presence of microbial mats in the Proterozoic has been taken to provide one explanation of the lack of preserved near-surface activity [trace makers would be excluded from the sediment by the mat (Seilacher, 1999)], it is clear that not

all sediment surfaces were covered by such mats, and their very presence would, as argued above, actually enhance trace fossil preservation where it occurred. Indeed, it should be stressed that whereas the preservation of Ediacaran body fossils seems to have been intimately connected with such mats (Gehling, 1999), which restricts their appearance in most sections to a few horizons only, trace fossils, conversely, are typically found in a much wider range of horizons, including those where there is no indication of sediment binding.

(ii) As noted earlier, the possession of a coelom and bilateral body architecture is not a prerequisite for burrowing—several cnidarians are efficient burrowers (Jensen, 1992), as are nemerteans, which lack a coelom functioning in this way (Turbeville & Ruppert, 1983; Turbeville *et al.*, 1992). Even before the evolutionary origins of bilateral animals, then, one might expect a trace fossil record. It frequently has been pointed out that some globular Ediacaran fossils are similar to plug-shaped Phanerozoic burrows interpreted as of cnidarian origin (Seilacher, 1984; Fedonkin & Runnegar, 1992). These may indeed be analogous in as much as they reflect, more or less, the lower surface of the producer. However, whereas most Phanerozoic forms are true burrows, the terminal Proterozoic forms are more likely to be impressions of organisms living on or close to the sediment surface. Possibly, then, burrowing cnidarians did not evolve until the Cambrian, in what may have been a response to increasing diversity of bilaterians and perhaps pressure from predation. Given that conditions that favoured the preservation of Ediacaran cnidarians are likely to have existed before the terminal Proterozoic, the trace fossil record thus implies a late origin even for burrowing cnidarians. This is significant because modern cnidarian phylogenies tend to place the holobenthic anthozoa at the base of the cnidarian clade (Bridge *et al.*, 1992; Schuchert, 1993). Such a lack of traces is thus consistent with a relatively late origin of crown-group cnidarians.

(iii) Although functional adaptations such as the coelom may not have arisen specifically as an improvement for burrowing, they represent such an important functional preadaptation to the burrowing life-style that infaunal ecologies (for the emerging stem-group bilaterians) surely would have been soon exploited. For example, even errant polychaetes such as *Nereis* are excellent burrowers, and early walking animals must also be expected to have been able readily to exploit the infaunal realm. This is true even if the presumed widespread

microbial mats provided a plentiful food-source for the emerging bilaterians (Seilacher & Pflüger, 1994). In the presence of a plentiful food supply, there would still be no barrier to exploitation of the infaunal realm. Further, as noted above, microbial mats, even if widespread, could hardly have been universal, with deeper water settings in particular being likely to lack them.

From the above, we conclude that the appearance in the fossil record of trace fossils represents a maximum time of origin of crown group bilaterians. The earliest trace fossils could have been made by cnidarians or ciliated organisms: but the likelihood of bilateral animals arising before any sort of trace fossil record began seems remote.

(c) Limits of trace fossil preservation

We have argued above that early bilateral animals, and perhaps early cnidarians, would have been able to make traces. We have presented arguments to show that their shallowness, and the probable presence of algal mats would not prevent preservation, and the latter could indeed enhance it. One other factor to consider, then, is size: were the earliest trace makers too small to leave trace fossils that could be detected in the record? The lower limit of the size of trace fossils in the record is surprisingly small. Trace fossils with a diameter of only 0.1–0.3 mm are known from bed-soles in the terminal Proterozoic and Cambrian (see Fig. 27B in Jensen, 1997; Narbonne & Aitken, 1990). Although preservation of such fine structures naturally requires exceptionally low diagenetic alteration of rocks, suitable sediments are far from rare in terminal Proterozoic and Cambrian sequences (cf. Knoll & Carroll, 1999). Further, meiofaunal influence on sediment (Reichelt, 1991) should potentially be detectable (Green & Chandler, 1994; O'Brien, 1987), even in the absence of discrete trace fossils. The size-limit for preservation of surface creeping animals is less clear. Even so, nemerteans, fractions of a millimeter in diameter leave clear grooves when moving over a sandy bed (S. Jensen, personal observations).

To summarise: we are arguing that if burrowing metazoans predated the first preserved trace fossils, then their upper size limit must have been approximately 0.1 mm in diameter, which places severe constraints on their evolutionary functional morphology (see above). On functional grounds, the assembly of typical bilaterian metazoan features could not have taken place in such an animal.

Typical bilaterian features are thus likely to have appeared first in animals that were already of significant size, implying that the evolution of such features cannot have significantly predated the first trace fossils of approximately 550 Ma. Even if one adopts the phylogenetically implausible view that body-plan features are virtually all convergences between the phyla, the first crown-group bilaterian must have had certain minimal features such as a relatively complex musculature, some sort of anterior condensation of nervous tissue and bilaterality (cf. Ax, 1985). Even at this level of organisation, organisms can generally make trace fossils, and they are structurally and physiologically capable of attaining relatively large size, typically by elaboration of internal cavities in order to reduce diffusion distances. The upper size limit is unclear even in a flatworm-like organism, with flatworms up to 60 cm in length existing today (and in diploblasts it appears to be virtually non-existent), but it is clearly well over 1 mm in diameter (cf. Clark, 1964). An animal this size would certainly leave trace fossils large enough to be detected easily in the fossil record, which can preserve trace fossils an order of magnitude smaller than this. Nevertheless, such arguments are provisional because the potential effect of low oxygen levels must also be taken into account.

(d) Oxygen levels and early animals

A consistent case has been argued for low oxygen levels providing a 'lid' on metazoan evolution, most recently by Knoll & Carroll (1999). This argument has two distinct components: first that metazoans themselves could not have evolved in very low oxygen levels (e.g. Towe, 1970), and secondly that large size in metazoans was prevented by low oxygen levels (e.g. Nursall, 1959; Raff & Raff, 1970; Runnegar, 1982*b*, 1991*a*). One of the reasons that free oxygen is important is its reported role in the synthesis of collagen (by being involved in the hydroxylation of proline) an obviously essential component of metazoan tissues such as muscle. It is therefore generally agreed that metazoans could not have evolved if oxygen levels were lower than approximately 1% of present atmospheric levels (PAL) of oxygen (PAL is approximately 160 mm Hg). Raff & Raff (1970) calculated the maximum tissue thickness that organisms can have under various oxygen tensions and use. For organisms that rely purely on diffusion, a tissue thickness of merely 0.1 mm is possible at 1% of PAL. For the

acoelomate organization, this would imply a body diameter of twice this (Cloud, 1976). However, in organisms with respiratory and circulatory systems such as the annelids, much greater tissue thicknesses are possible; and with a central fluid cavity, there seems to be no obvious limit on potential body size. For example, the large polychaete *Arenicola* can survive in oxygen levels as low as approximately 4% PAL (see Raff & Raff, 1970 and discussion in Cloud, 1976), although it probably cannot live permanently under such conditions (Schöttler & Bennet, 1991).

These basic data need to be compared with potential models for both basal bilaterians and for oxygen level changes through the Proterozoic. Nursall's (1959) original model went out of favour because new views of Proterozoic oxygen levels suggested that relatively high levels had been attained quite early on (Runnegar, 1991). Secondly, these data imply that even if bilaterians evolved at the lowest possible oxygen levels [i.e. at the collagen synthesis threshold (the Towe limit) of approximately 1% PAL] and were reliant entirely on diffusion, they would still potentially be large enough to leave a trace fossil record. Thirdly, if a minimal bilaterian ancestor is adopted (implausibly, because it would imply that virtually all bilaterian features have been acquired convergently), as discussed above, it would still have certain important features. Taking the acoel flatworms as a model (Ruiz Trillo *et al.*, 1999), the animal would still possess bilateral symmetry, some sort of central nervous system, mesoderm and relatively complex musculature. Even at 1% PAL, the above data suggest that this animal would thus also have the structural capability to leave a detectable trace fossil record. However, this extreme minimalist scenario suffers from the following three flaws. First, as noted above, there is no reason to think that the ancestral animal was so minimal, as that would imply a highly unparsimonious distribution of characters such as the coelom, BVS, segmentation, nephridia and so on. Secondly, the implied presence of muscle in such an animal is a structural adaptation that is not subject to the strictures of oxygen levels in that low oxygen levels would not lower the size of animals that one would expect to possess muscle: it is a mechanical rather than a physiological feature (although the activity of muscle may demand higher oxygen levels). Because the cilia-muscle transition seems to occur in animals somewhat bigger than 1 mm in length (cf. Sleight & Blake, 1977), it follows that such muscle must have originally evolved in an animal of this size or greater. Even if the ancestral bilaterian

was of this minimal grade of organization then it can still be inferred to have been large enough to make trace fossils. Thirdly, even flatworms can reach relatively large size, because of their highly branched gastrovascular system which minimises tissue thickness in all parts of the body. Like cnidarians, which are effectively only two cells thick, the body architecture of flatworms can allow them to attain considerably greater size than that implied by the strict limits of oxygen levels. Extremely low oxygen levels would not act to keep even such minimal organisms at tiny size. Finally, although Proterozoic oxygen levels remain highly uncertain, and no doubt also fluctuated, an appreciable amount of oxygen seems to have accumulated by 2 Ga (e.g. Kasting, 1991; Canfield & Teske, 1996). By 1 Ga, perhaps 5–6% PAL had accumulated (Canfield & Teske, 1996) – considerably greater than the Towe limit (Towe, 1970). One might also note that the entire question of oxygen usage is a complex one, and models of physiological requirements of Proterozoic organisms (e.g. Runnegar, 1982*b*, but see also Runnegar, 1991*b* for a more comprehensive view) inevitably fail to take into account some important features (see contributions in Bryant, 1991). For example, extant organisms have a complex range of responses to low oxygen level conditions, including the varying use of anaerobic respiration pathways and the slowing down of metabolic rates. Indeed, although relatively little comparative data exists from extant organisms, there are indications that general oxygen usage is in itself environment dependent. Nematodes living in low oxygen environments, for example, have been shown to have lower rates of respiration than those living in more oxygen-rich environments (Ott & Schiemer, 1973; Warwick & Price, 1979; Atkinson, 1980); whether or not this lower oxygen requirement is because of more efficient metabolism or because of some use of anaerobic respiration is not clear. The role of anaerobic respiration in Proterozoic animals is almost entirely uncertain. Nevertheless, stem-group and early crown-group bilaterians would surely have inherited important anaerobic respiratory pathways from their ancestors [such pathways being present in sponges and cnidarians (Runnegar, 1991*b* and references therein; Hochachka & Somero, 1973; Hammen, 1973)], especially given the low oxygen levels they would have lived in. The clear implication is that late Proterozoic animals would have had lower oxygen demands than many extant forms. If so, then calculations of the limits placed on body size by oxygen levels (e.g. Runnegar, 1982*b* for *Dickinsonia*)

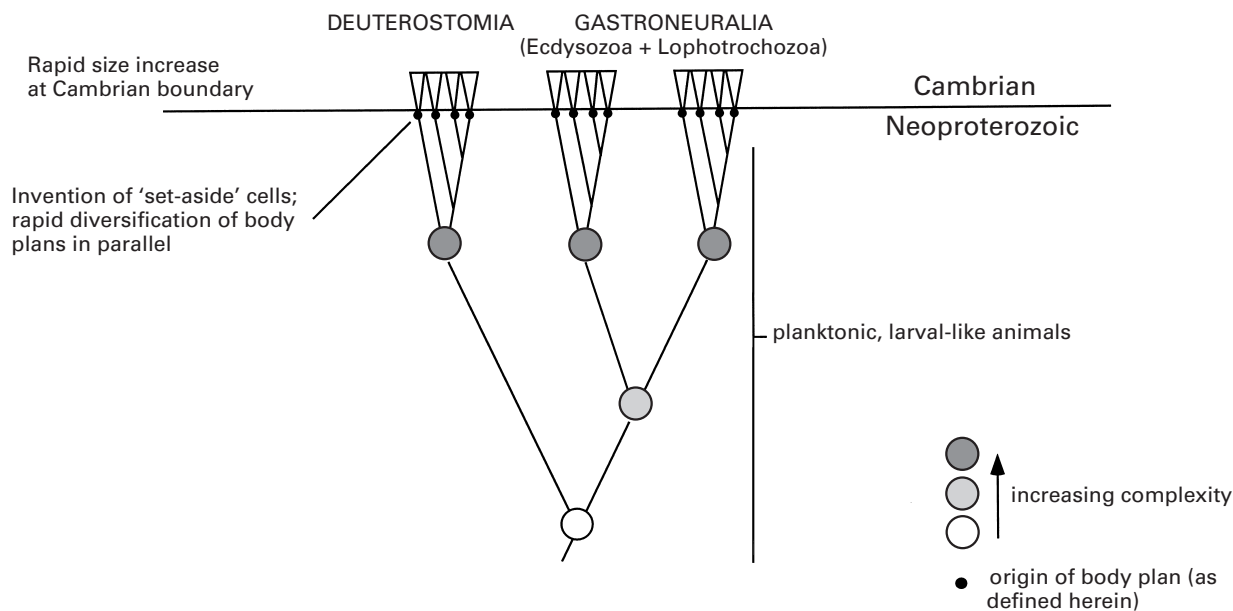


Fig. 10. The scenario for early bilaterian appearances of Davidson *et al.* (1995) and Peterson *et al.* (1997). Early bilaterians are simple, with only 'Type I' embryogenesis, and broadly organized like extant trochophoran larvae. When set-aside cells and the associated 'pattern formation' developmental package have been constructed, a complexity threshold is passed that allows the explosive radiation of body plans in the Cambrian.

may be suspect. Runnegar (1982*b*) suggested that, on the basis of its likely size and thickness, and taking an average oxygen consumption rate per gram of tissue, *Dickinsonia* must have had some sort of circulatory system; and its peculiar flattened geometry despite this advantage pointed to low oxygen levels in the late Proterozoic. He later revised this calculation considerably (Runnegar, 1991*b*), but still concluded that the oxygen requirements of the organism were too great for it to rely on simple diffusion. Nevertheless, considerable caution must be exercised in interpreting these results: if the animal had a sizeable body cavity (e.g. a gastrovascular system or a coelenteron), its potential for large size even under low oxygen conditions would be considerably enhanced, and if it could partly rely on anaerobic respiration, its oxygen requirements would be cut further.

In summary, given the uncertainties pertaining to Proterozoic oxygen levels, the metabolic rate of early animals and the degree of their ability to respire anaerobically, together with the size calculations discussed above, it does not seem at present that low oxygen levels may be invoked to explain the absence of large animals in the Proterozoic. Low oxygen levels could restrict animal size either by ruling out some essential synthetic process (e.g. collagen synthesis), or because diffusion distances were limited, or by ruling out certain types of metabolic activity

(e.g. muscle activity). From phylogenetic analysis it is clear that the last common ancestor of the bilaterians possessed muscles, and must thus have evolved at levels of oxygen high enough to permit their use. This phylogenetically inferred oxygen level is higher than the collagen synthesis threshold. More important, it implies that the animal in question was large enough to have evolved muscles, which in turn implies millimetric body size at minimum (Sleigh & Blake, 1977). The question of diffusion distances is thus not strictly relevant: an ancestral organism less than 0.1 mm in diameter is not compatible with it also having evolved complex musculature. Either oxygen levels were not that low, or the animal had various strategies for dealing with low oxygen levels such as anaerobic respiratory pathways or a complex internal body cavity. Nursall's (1959) original argument, even as modified by Runnegar (1991*b*) seems to fail on this account.

(4) Developmental thresholds?

The second view to be discussed is that extant phyla emerged suddenly at the base of the Cambrian, after important thresholds in developmental complexity were achieved in animals with maximal indirect development (Fig. 10; Davidson *et al.*, 1995; Peterson *et al.*, 1997). The ancestral forms are considered to be tiny and simple, akin to plankto-

trophic larvae of many extant forms, and patterned with a limited developmental program termed Type I embryogenesis (Davidson, 1991). The evolution of complex adult structures seen in the Bilateria had to wait for the invention of 'set-aside cells' from which complex body structures form, patterned by a novel developmental apparatus termed 'pattern formation'. In so far as evolution of adult body plan is essentially the result or reflection of reorganization of development, investigation of how these changes take place is of considerable importance and value, and our intention here is not to offer a direct critique of this approach. Another point of merit of Davidson *et al.* (1995) is their recognition that character evolution can take place partly decoupled from cladogenesis (cf. Fortey *et al.*, 1996). Nevertheless, like the first view, this hypothesis raises several problems. Three issues need to be addressed: first, is maximal indirect development as widespread as the authors suggest, and is it plausibly primitive for the bilaterians? Secondly, is the scenario ecologically plausible? Lastly, is the scenario in accord with the known distribution of characters in bilaterians and their sister group, the cnidarians?

(a) Primary planktotrophy?

Of the three large groupings of animals currently fashionable – lophotrochozoans, ecdysozoans and deuterostomes (Balavoine & Adoutte, 1998) – a good case can be made for the second of these not possessing primary planktotrophic larvae, and for at least this important group of bilaterians, and for the origins of their body plans, the proposals of Davidson *et al.* (1995) are unlikely to be applicable: animals such as nematodes, arthropods and priapulids must have developed from an organism that was a direct developer. Indeed, Haszprunar, Salvini-Plawen & Rieger (1995) argue that planktotrophy is not primitive for bilaterians as a whole. However, such an assessment rests largely on the possibility that the evolution of larval types could be convergent. We have argued above that convergence can only be demonstrated phylogenetically, and to assume that two structures are not homologous despite their similarity appears to be methodologically suspect (but see also Conway Morris, 1998*b* for a more sympathetic view). A more complex critique of the view that planktotrophy is primitive within the Bilateria is provided by Olive (1985). Effectively, the argument is that planktotrophy is not an independent trait, but is correlated with a host of other reproductive features including body size, fertili-

zation mode and egg size. His conclusion was that planktotrophy is a feature of large, not small animals, and he thus undermined the theory of Jägersten (1972) which posited a tiny ancestral form which was nevertheless planktotrophic. Nielsen (1995, p.15) attempts to meet this criticism by arguing that at the base of the Cambrian, when the larval-animals are postulated last to have existed, planktonic predation was virtually non-existent, and thus enormous bursts of gametes into the water (requiring large body size to store them before release) would not be necessary. Apart from its *ad hoc* nature, this defence fails to address the purely spatial problems of ensuring that egg and sperm meet in an external aqueous environment. This criticism can also be aimed at Davidson *et al.* (1995), because however the theory is interpreted, the ancestral bilaterian in which 'pattern formation' arose was small and became an indirect developer, a contradictory pairing. Indeed, the whole question of how such hypothetical larval-animals could reproduce is raised in an acute form, given that, by hypothesis, their gonads had not yet evolved: germ cells are formed from set-aside cells (e.g. Peterson *et al.*, 1997). It might therefore be possible to argue that these ancestral forms really had a type of direct development, using a now-lost reproductive system. However, this (i) would imply that the gonads and even gametes of bilaterians are not homologous to those of their outgroup, the cnidarians; (ii) raises questions of how the switch from one reproductive system to another took place. Conversely, if the germ cells have always been formed from set-aside cells patterned by bilaterian-style development and thus were present even in the earliest stem group bilaterians (as suggested in Peterson *et al.*, 1997 for their existence in the otherwise larval-like rotifers), then the origins of complex adult plans cannot be correlated with the origin of pattern formation *per se*.

Even if the last common ancestor of protostomes and deuterostomes (LCA) had indirect development and possessed a planktotrophic larva, as is generally considered to be the case (Conway Morris, 1998*b*), it is not valid to move from this relatively uncontroversial statement to the more controversial claim that the last common ancestor was in essence a larval-like animal that had not developed pattern-formation development. Indeed, the authors of the theory themselves retreat somewhat on this point: Davidson *et al.* (1995) advance the hypothesis that bilaterian animals evolved from planktonic animals similar to larval stages today, whereas in Peterson *et al.* (1997), more stress is simply placed on the shared

developmental characteristics of protostomes and deuterostomes. This latter stance is consistent with the view that the LCA was a benthic organism with indirect development and a planktotrophic larva, and seems a sounder stance to take, but in doing so the explanatory power for the alleged sudden appearance of body plans (without intermediates) in the Cambrian is greatly reduced. Further, if this latter view is taken, then arguments about the distinctness of adult body plans of the extant phyla (Peterson *et al.*, 1997) are beside the point, because adult body plan homologies are consistent with set-aside cells having evolved before the LCA (see below). Two critical questions thus seem to be: (i) did the ancestral stem group bilaterians only have direct development finishing at a level of organization similar to the extant planktotrophic larvae, or did they also possess an adult body plan that possessed homologies with the adult bodies of both cnidarians and extant bilaterians? (ii) If 'pattern formation' evolved in the bilaterian stem lineage, did the deployment of such developmental mechanisms into the formation of complex adult structures take place before or after the LCA?

(b) *Is the hypothesis of Davidson et al. (1995) ecologically and phylogenetically plausible?*

If the primary planktotrophic larva is primitive within the Bilateria and indeed represents the ancestral form of the Bilateria, the original hypothesis of Davidson *et al.* (1995) must face charges of being unparsimonious, in that it implies virtually all of the features of adult bilaterians were obtained in parallel from one phylum to the next. For example, Peterson *et al.* (1997) illustrate two pairs of phyla (echinoderms and enteropneusts and echiurans and annelids) which have very similar larvae but very different adult bodies. In the first case, although the adult body plans are different, it can be argued that they nevertheless possess morphological homologies such as the axial complex (Nielsen, 1995), and given that hemichordates may be paraphyletic (Nielsen, 1995; Salvini-Plawen, 1998), the clear implication would be that echinoderms did in fact evolve from a hemichordate-like worm, in apparent contradiction to the theory. Similarly, molecular and morphological evidence has been used to suggest that echiurans are in fact a member of the in-group of the annelids (Nielsen, 1995; McHugh, 1997, but see Haszprunar, 1996 for an alternative view), again implying that echiurans evolved from an organism that was in fact a crown-

group annelid. An alternative scenario would thus be that the last common ancestor had a larval type (planktotrophic) that has been conserved in the two lineages, whereas the adult body plans have diverged, which points to the important possibility that a planktonic larval stage, simply because of its different life style to the adult, might experience consistent adaptive pressures on it, even if the adult undergoes a radical ecological shift (or *vice versa*).

Secondly, the theory fails to provide an ecological setting for the evolution of adaptive morphology. It should already be clear that we regard functional and ecological considerations of prime importance with regard to the assembly of bilaterian phyla. In extant phyla, the transformation of a planktotrophic larva generally begins before settling, i.e. adult features such as nephridia, segments and appendages start appearing before the animal switches to a benthic life style. On the literalist reading of the life cycle as recapitulation that this theory partly relies on, the implication would be that there were at some stage planktonic larval-animals that had developed complex adult features appropriate to the benthos without ever coming into contact with it: and it is hard to see the adaptive or ecological significance of such developments, or why they would develop in so many lineages nearly simultaneously. Rather, as argued above, the appearance of muscle, coeloms, nephridia, segmentation and so on can only have evolved in a setting where they were adaptively useful and where the environmental challenges faced by the ancestral organism could have actually shaped their form. We thus agree with the comment of Valentine (1973, p. 420) that 'the groundplan features of phyla were originally functional adaptations... [which]... arose in response to a particular adaptive opportunity, which was associated either directly or indirectly with specific environmental relationships'. Although it has been argued that some features of bilaterians arose as adaptations to a nektonic lifestyle, such as the notochord and segmentation in chordates (Clark, 1964), many others are much more plausibly interpreted as benthic adaptations, such the hydrostatic coelom of annelids, and the bag-shaped bodies of sipunculans and priapulids. Indeed, many planktonic organisms today such as copepods represent considerable simplifications from the organisms they are presumed to have evolved from, and all metazoan members of the plankton, both extinct and extant, may be inferred to have evolved from benthic ancestors (Rigby & Milsom, 1996; cf. Signor and Vermeij, 1994).

The presence of such benthic features in the modern larva thus seems to imply a process of 'adulation', where adult features become incorporated into the larva (Jägersten, 1972; Nielsen & Nørrevang, 1985), implying that morphological and ecological ancestry cannot simply be 'read off' from present day developmental routes. Given the views we have expressed above about developmental timing changes giving rise to morphologically different structures (e.g. the enterocoel and schizocoel), we suggest that similar changes may be inferred to have occurred in the evolution of planktotrophy as well. In the terminology of Davidson *et al.* (1995), this would imply that responsibility for patterning particular morphological features could have shifted even from Type I embryogenesis to the more derived 'pattern formation' and back, whilst the morphological features themselves persisted relatively unchanged. A putative example of this sort of shift is provided by the musculature in cnidarians and bilaterians, which despite differences, may be homologous. In cnidarians, presumably only possessing Type I embryogenesis at most, the muscles must be formed by this process; but in bilaterians, the muscles are now what we choose to call mesoderm and are thus, by hypothesis, patterned by the later 'pattern-formation' package. In other words, unlike in the scenario of Davidson *et al.* (1995), where the evolution of pattern formation necessarily preceded and indeed triggered the evolution of complex primarily mesodermal tissue types, we would suggest that the morphological features evolved first, being patterned by Type I embryogenesis, followed by increasing co-option of the concurrently evolving pattern-formation developmental package (see Budd, 1999a for discussion of developmental patterning of a particular structure shifting from one system to another). The key issue may be whether or not the limited developmental systems of cnidarians and larvae rigidly imply a definite constraint on the complexity of the morphology that may be generated by them, bearing in mind the injunction of Schwenk (1997, p. 260) that 'phenotypic and/or phylogenetic patterns as *prima facie* evidence of constraint should be avoided'.

To summarise: the developmental evolution model of Davidson *et al.* (1995) can be interpreted in two ways. The first way is that the LCA of the bilaterians was a larval-like planktotrophic organism that possessed undifferentiated set-aside cells; the story of body plan appearance in the Cambrian may be seen as the progressive and parallel elaboration of these cells in the various lineages leading to the body

plans we see today: in other words that although larval types are homologous, indirect development itself is not. This interpretation, similar to the 'trochaea' theory elaborated by Nielsen & Nørrevang (1985), although apparently favoured by Davidson *et al.* (1995) in that they emphasize larval over adult homologies, seems unlikely, because of its unparsimonious explanation of body-plan features such as the coelom, BVS, nephridia and so on. If the theory is interpreted as saying that stem group bilaterians were larval-like animals, but that the LCA of bilaterians was an indirect developer, then the extant body plans must have evolved from an animal with a relatively large benthic stage. Seen in this light, the theory does not add any extra understanding of the pattern of bilaterian evolution (in terms of offering an explanation of the alleged rapid appearance of body plans without intermediates), nor can it be seen as an explanation for molecular data suggesting bilaterian origins deep in the Proterozoic. Secondly, one may question whether the order of events in the model is indeed consistent with what is known about animal morphology, especially when cnidarians are considered, which suggests that at least some features of morphology evolved before the hypothesised acquisition of 'pattern formation'. Thirdly, the ecological and functional background to the evolution of the body plans of the extant phyla remains, in our view, a fundamental challenge to all theories that invoke microscopic and/or planktonic ancestors to the major clades.

(5) Cryptic taxa?

The final view, that the last common ancestor of bilaterians was a large and relatively complex animal, but simply has not been found in the fossil record (Fig. 11; Balavoine & Adoutte, 1998), takes seriously the apparently phylogenetically significant features shared by adult bilaterians. Indeed, such a view is hinted at by one of the studies that suggested a very early time of origin of bilaterians (Wray *et al.*, 1996). They point out that their data suggest that the echinoderm/chordate split took place around at least 1 Ga. If the coeloms of echinoderms and chordates are homologous, which would be widely accepted, and the sister group of echinoderms is one group of hemichordates (see above) then the implication would be that the last common ancestor of echinoderms and chordates was likely to be a relatively large, hemichordate-like worm. As a result, the view that three separate lineages of large animals

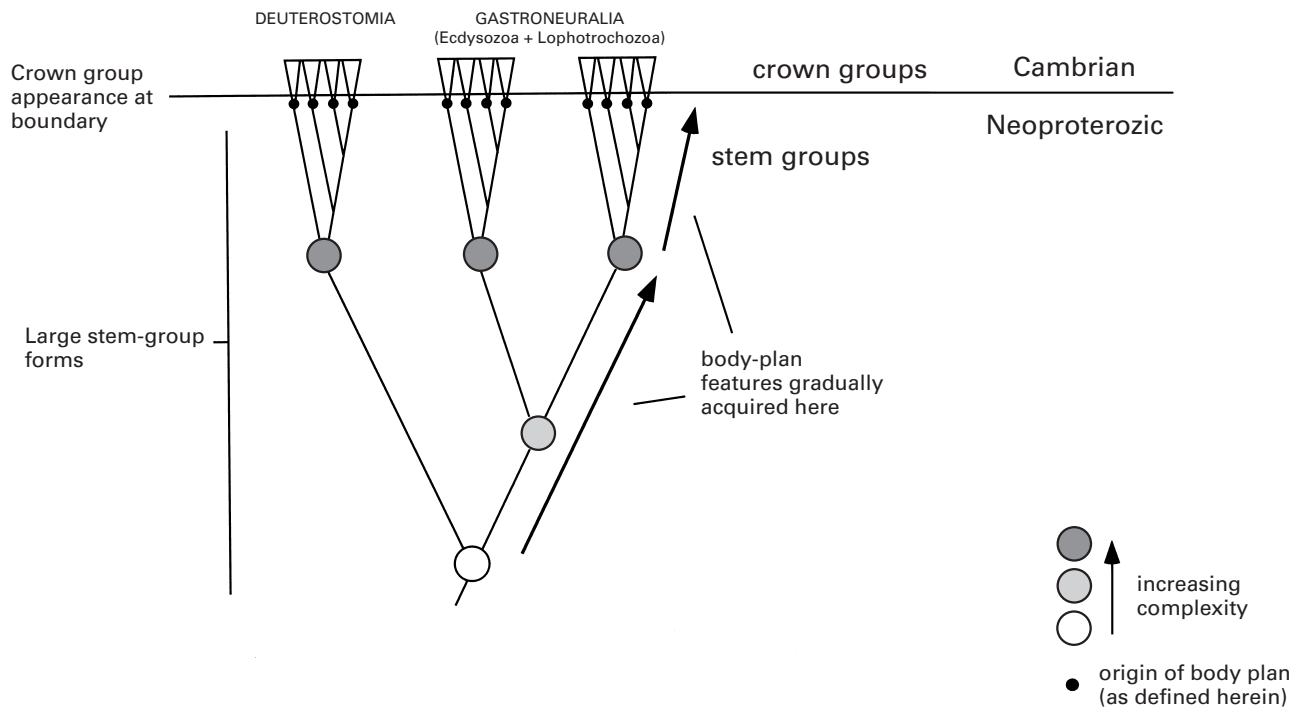


Fig. 11. The scenario for early bilaterian appearances of Balavoine and Adoutte (1998). Early bilaterians are large and complex, but are cryptic, living in rarely preserved habitats such as the deep sea. When they radiate at the base of the Cambrian, three distinct clades are recognizable.

would persist without leaving any fossil record for somewhere between 100 and 800 Myr on the grounds of 'rarity' or of inhabiting environments not represented in the fossil record is implausible, quite apart from difficulties associated with its *ad hoc* nature. Such animals would be coelomate and possibly segmented, be excellent trace fossil makers, and would by their very nature be ideal inhabitants of the marine benthos – which provides the bulk of the fossil record. It is possible that such animals were living in less well preserved environments such as the deep sea; but this raises separate problems such as what prevented these forms from radiating into shallow marine environments. The usual explanation for environmental restriction today – such as why crinoids are now found in deep water – is an ecological one. However, given that this scenario views the Cambrian explosion as a radiation in an 'ecological vacuum', it is very hard to see what prevented this radiation from occurring before. McIlroy & Logan (1999) argue that nutrient concentrations were lower in shallow water because of the higher sedimentation rates associated with a 'Tommotian high-stand', and that burrowers were excluded from the nutrients available by the presumably frequent arrival of sandy storm beds which the early, relatively inefficient burrowers were unable to penetrate. In this view, complex and large

animals evolved in deep water where storm beds were much less common, and after achieving a certain complexity were equipped to face the challenges posed by the shallow water environment. This scenario seems to rely on an unrealistic view of the frequency and effect of storm beds in shallow water, which by their nature are relatively infrequent events. It is hard to imagine the benthos being totally excluded by such events, or even being significantly affected by them. It is also hard to see how – in an ecologically empty world – such early lineages could have persisted as rare animals for such an enormous length of time, because this would require a precise balance between speciation and extinction to be maintained for this period. With only few numbers, one would expect either extinction or a rapid escalation (Strathmann & Slatkin, 1983). Given we know that some animals survived, the implication would be that countless lineages must have diverged in the long period of time before the fossil record commenced.

The view of three separate radiations is also problematic in that it treats taxonomic groupings of extant bilaterians as having had particular significance in the past: a case of the 'retrospective fallacy'. Even if there are three large plausible groupings that bilaterians today may be placed in, in the past there would have been many more lineages

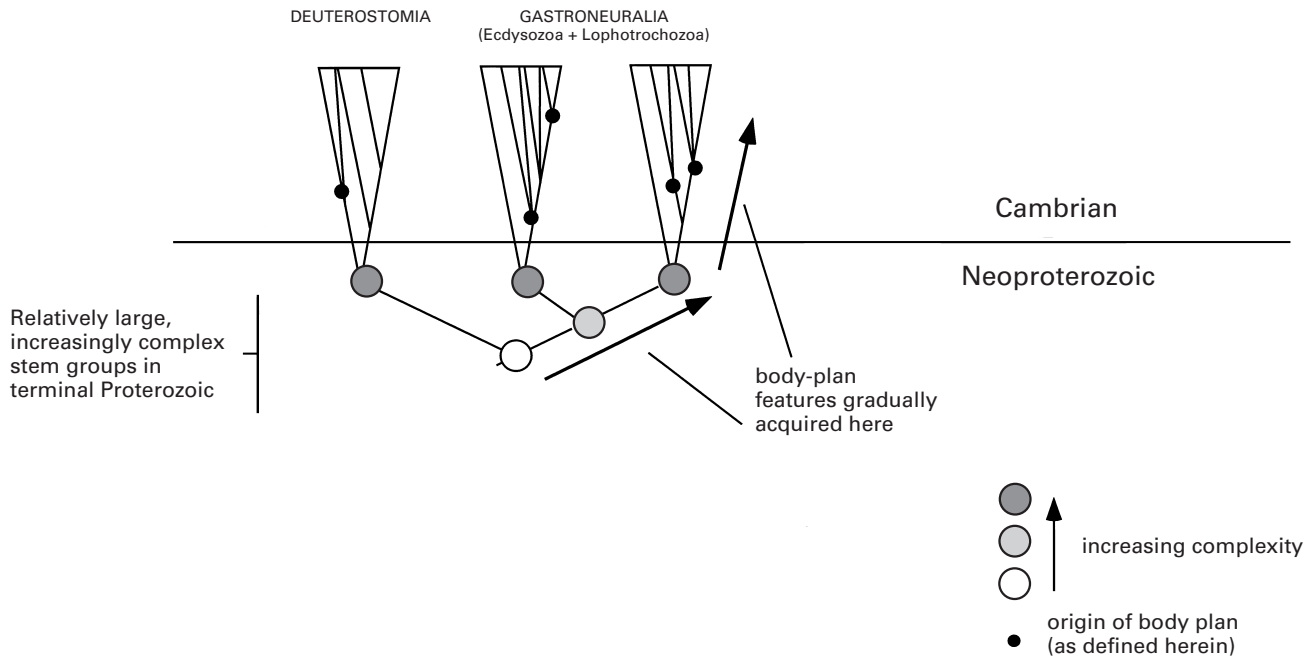


Fig. 12. The model proposed herein for body-plan origins. Stem-group bilaterians originate and radiate in the terminal Proterozoic, with the body plans of extant phyla not being achieved in general until well into the Cambrian or later.

of equal significance. A late Precambrian systematist would not have recognized a three-fold nature in the unfolding evolutionary radiation. In other words, simply because three major groupings have happened to survive until the modern day, this cannot be taken to imply, as Balavoine & Adoutte (1998) do, that basal members of these clades were somehow more diversified or significant in the past, and that members of clades that did not survive were necessarily 'poorly diversified' in the Cambrian.

(6) History of the bilaterians

As the above discussions aim to show, there are serious difficulties associated with all the major arguments for an extensive Precambrian bilaterian history. We thus support the 'late origin' model of metazoan origins (Valentine, 1973; Valentine, Erwin & Jablonski, 1996), with the important refinement that extant body plans of phyla did not in general become established until during or potentially well after the Cambrian explosion itself (Fig. 12). This recognition of significant degrees of Phanerozoic body-plan evolution significantly takes the pressure off the period around the beginning of the Cambrian as a time when all major innovation occurred, and also removes an important reason for postulating a deep origin of the metazoa. This view is supported by the presence of large animals in the Cambrian – such as halkieriids (Conway Morris &

Peel, 1995) and anomalocaridids (Budd, 1996, 1997, 1998a) that can be used to reconstruct the routes that phylum-level evolution took.

The Cambrian explosion, in this view, is truly a Cambrian phenomenon, not a Precambrian one. We recognize that this view of bilaterian evolution is at odds with recent molecular clock data (which in itself shows a high degree of variation: see Conway Morris, 1997; Ayala & Rzhetsky, 1998; Ayala, 1999), but we would stress that the evidence and arguments we have presented above amount to more than merely 'negative evidence'. Rather, we would argue that proponents of deep origins of the bilaterians must be able to account realistically for the facts of the fossil and trace fossil record if the arguments are to be accorded a status more than being merely *ad hoc*. The trace fossil record in particular, together with the implied limitations on body size and ecology, places severe constraints on what sorts of animals were living in the Precambrian, which needs to be taken into account in any theory of bilaterian origins.

(7) Cladogenesis versus ecological diversification: what does the Cambrian explosion represent?

In a somewhat neglected paper, Raup (1983) argued on mathematical grounds that clade divergence of large extant groupings would necessarily occur early

on in metazoan evolution. If true, then the Cambrian explosion as such does not require a particular explanation, but was simply the consequence of the origin of the metazoans some time in the late Proterozoic, a view championed some 30 years ago by Preston Cloud (Cloud, 1968). Indeed, we recognize above the existence of many lineages relatively early in the Cambrian. Raup (1983) points out that this view of cladogenetic pattern does not address the other, ecological aspect to the Cambrian explosion: why do extant body plans become fixed so soon in these lineages? From the above, we would argue that this problem is based on an incorrect interpretation of the Cambrian fossil record. Representatives of many lineages are indeed present – as predicted by Raup (1983) – but the modern body plans (as defined phylogenetically) are rarely established so early. Ecological innovation seems thus to have continued throughout at least part of the Phanerozoic, even if some degree of ecological constraint did eventually curb innovation in the marine benthos. Nevertheless, in other realms such as the plankton (Rigby, 1997; Rigby & Milsom, 1996), the meiobenthos and the parasitic realm, quite different rules may apply (cf. Signor & Vermeij, 1994). It is likely that taxa (including phyla) have been repeatedly recruited into these realms over a long period of time. Ecologically, the Cambrian explosion – of coelomate hard-part-bearing animals – may thus have been primarily a benthic phenomenon, and there may not have been a concurrent ‘parasitic’, ‘meiofaunal’ or ‘planktonic’ explosion unless there was ecological linkage between the two (as in the scenario envisaged by Butterfield, 1997). This incidentally also provides a warning against using phyla with substantial hard parts as a proxy for phylum appearance time overall. Taxa with hard parts are generally associated with the benthos. Whilst it appears to be true therefore that Cambrian benthic ecology was broadly established rather early (cf. Conway Morris, 1986), it is not valid to infer from this that other phyla associated with very different ecological settings had evolved concurrently, another common assumption (Knoll & Carroll, 1999). Significantly, hard-part-bearing taxa such as molluscs that are known to have invaded the pelagic realm do not seem to have done so before the end of the Cambrian. In particular, the fossil record is consistent with the several crown-group phyla found in the meiofauna such as the loriciferans and nematodes having originated at almost any time in the Phanerozoic, including very recently.

V. ORIGINS OF THE BILATERIA

If a deep origin of the bilaterians is unlikely, is there any evidence from the fossil record of how they evolved? Recalling the logical division of the animal kingdom into phyla, stem groups to phyla, and stem groups to groups of phyla, it is clear that Precambrian and Cambrian metazoans can only be placed in a very few positions relative to extant phyla (Fig. 13). An example of an Early Cambrian fossil in the crown group of a phylum would be *Lingulella* the lingulate brachiopod. Much more common would be a placement in the stem group of an extant phylum, such as *Anomalocaris* for the arthropods, *Wiwaxia* for the annelids and perhaps *Gogia* for the echinoderms. Are there any taxa that lie in the stem groups of groups of phyla? Identification of such taxa might be difficult because it would partly rely on reconstruction of the ground plans of last common ancestors of groups of phyla, a subject fraught with controversy. Nevertheless, some coeloscleritophorans may lie in the stem group to a large array of protostomes (Conway Morris & Peel, 1995); and some of the Cambrian lobopods lie in the stem group of onychophorans + tardigrades + arthropods (Budd, 1996). Taxa that might be placed even more deeply include *Yunnanozoan*, which continues to be

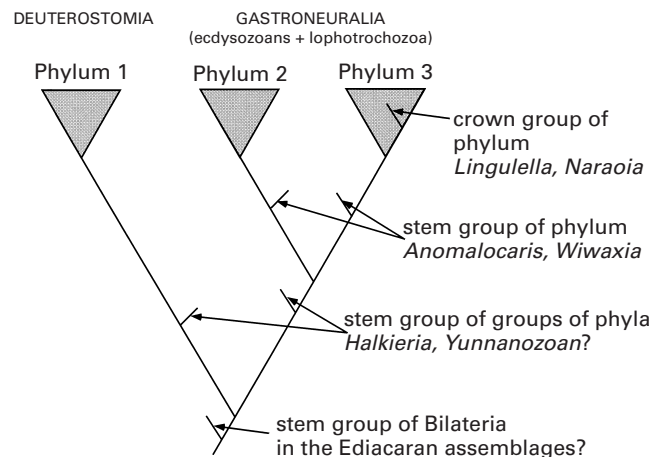


Fig. 13. The logical possibilities for placement of problematica in the terminal Proterozoic and Cambrian. Each major grouping of bilaterians is shown schematically by a single phylum. Given the presence of sponges and cnidarians (stem or crown group as yet largely undetermined) by at least the Early Cambrian, the only sector of the metazoan tree not represented are stem group bilaterians. This suggests on methodological grounds that some Ediacaran taxa may lie here, because there is no theoretical reason why stem-group bilaterians would be less easily preserved than other segments of the metazoan tree.

problematic despite apparently possessing some deuterostomic features (Chen *et al.*, 1995; Dzik, 1995; but see also Bergström *et al.*, 1998 for a critique of this view); and perhaps some of the 'aschelminth' taxa (e.g. Hou & Bergström, 1994) which conceivably lie near the base of the entire Ecdysozoan clade.

Given the existence of sponges and cnidarians early on in the fossil record, the most striking gap in coverage of the metazoan tree by the body fossil record is that of stem-group bilaterians. Why have these forms apparently not been preserved? If the flatworms are to be removed from their traditional position at the base of the tree, or at least are seen as being morphologically derived [marking in effect the return to fashion of continental 'archicoelomate theories' (Rieger, 1985; Rieger *et al.*, 1991)], then the question of what the last common ancestor of cnidarians and bilaterians looked like is raised again. With the possible exception of the ctenophores, whose systematic position remains highly uncertain, there are no obvious extant candidates for basal bilaterians (Adoutte *et al.*, 1999) except for the acoels (Ruiz Trillo *et al.*, 1999), which have recently been placed deep in the clade by some (but not all) analyses. However, as they appear to be monophyletic, there is no basis for optimizing all of their distinctive acoelomate morphology to be synapomorphies of all bilaterians, even if they may offer clues as to how some features such as the nervous system evolved. Further, they do not offer clues to the morphology of the last common ancestor of protostomes and deuterostomes, a split that is dated by molecular clock data.

Despite the current uncertainty over the morphology of the bilaterian ground plan, the most obvious candidates for the stem group of the Bilateria should be looked for in the Ediacaran assemblages, simply because plausible fossil candidates for all other sectors of the metazoan tree exist (e.g. stem-group cnidarians, stem-group deuterostomes, crown-group poriferans etc), and there is no theoretical reason why stem-group bilaterians should not also be represented. This proposal has several advantages. First, the Ediacaran biota exists at a time when, in the model proposed here, stem group bilaterians would be expected to be diversifying. Secondly, some of these fossils, although enigmatic, share certain features in common with both cnidarians (some are radially symmetrical) and bilaterians. Thirdly, large cnidarians exist which nevertheless lack important bilaterian features such as nephridia, complex musculature and nervous systems and

complex vascular and respiratory systems. Even if extant cnidarians are monophyletic (being united by features such as the cnidicils), they may still be representative of a grade of late Precambrian organization from which bilaterians evolved (cf. Buss & Seilacher, 1994), implying that some large Ediacaran fossils may represent different stages in the acquisition of bilaterian features from a cnidarian-grade ancestor. This may be significant in that the radiation of Ediacaran forms seems significantly to predate the first trace fossils (Fig. 7). On the other hand, the appearance of trace fossils broadly coincides with the appearance of diverse Ediacaran assemblages, which include reasonable candidates for bilaterian body fossils of unclear affinity, whereas such candidate bilaterians are missing in an older assemblage of Ediacaran fossils (Gehling *et al.*, 1999). Given that the cnidarian-bilaterian transition is notoriously hard to imagine, it is therefore difficult to exclude the enigmatic Ediacaran fossils from this systematic position on the grounds that they do not look like stem group bilaterians. Nevertheless, we stress that we are not suggesting here that any *particular* Ediacaran fossils are in fact stem group bilaterians, merely that there are methodological reasons for thinking that some may be.

VI. CONCLUSIONS

(1) A primary aim of palaeontology is – or should be – the reconstruction of stem groups, so that the order of assembly of crown group features may be discovered (Smith, 1994). Rigorous application of this procedure to the origin of the bilaterian phyla demonstrates that, far from being monolithic blocks, the extant phyla were demonstrably assembled over a period of time, mostly stretching well into the Phanerozoic. The body plans with which we now associate the phyla must therefore also have arisen over an extensive period of time in the Cambrian and later. Even if the Cambrian explosion consisted of a period of highly elevated cladogenesis (a phenomenon predicted by modelling of diversification patterns), it does not seem to have been quite so morphologically and ecologically dramatic as is usually depicted: not because of significant Proterozoic events, but because of significant Phanerozoic events. Indeed, recent emphasis on the Ordovician radiation, which in some accounts is as significant as the Cambrian one (Droser, Fortey & Li, 1996) is entirely in accord with this view. Phyla may be a useful way of viewing the diversity of

extant taxa, but become a typological hindrance in understanding its origin. Virtually all zoology text books perpetuate this problem by referring to the ‘sudden origin of phyla at the base of the Cambrian’, a misinterpretation of the fossil record based on this sort of typology.

(2) Theories of deep Proterozoic origins of bilaterians ultimately rest on disputed molecular data. There are good reasons to suppose that the last common ancestors of groups of phyla were themselves relatively large differentiated animals that would have left a fossil record: theories invoking tiny ancestors in either the plankton or meiofauna may be refuted on functional and adaptive grounds. Theories of deep origins of bilaterians that rely on body-plan features evolving early in tiny animals can be refuted on the grounds of functional evolution; theories that rely on late origins of body-plan features may be refuted on the grounds of parsimony, and on the grounds that even tiny, simple ancestors should have left some sort of trace fossil record.

(3) Although the morphology of the last common ancestor of the Bilateria remains unclear, the common assumption that the features of the extant phyla are multiple convergences (Thomas, 1998) is unjustified on methodological grounds; convergence could only be conclusively demonstrated by phylogenetic analysis. A theory is presented to explain the diversity seen in just one feature, the coelom, relying on changes in developmental timing, which underpins its monophyletic origin.

(4) Most Cambrian taxa in fact fall into the stem groups of extant phyla, and there are also several candidates for falling into the stem groups of even larger clades. The apparent lack of intermediates between cnidarians and bilaterians suggests that some of the enigmatic Ediacaran taxa may be stem group bilaterians, and some features of their morphology support this view: nevertheless, phylogenetic analysis of their systematic position has yet to yield firm results either way.

(5) The terminal Proterozoic and Cambrian fossil record does not offer a steady-state picture of metazoan life, as would be expected if the major cladogenetic events had occurred deep in the Proterozoic. Rather, both the trace fossil and body fossil records suggest a steady stratigraphic diversification of form and function from the latest Proterozoic up into the Phanerozoic, even if the phylogenetic threads connecting the Ediacaran assemblages with the Phanerozoic ones remain currently tenuous. In particular, the early Cambrian record is dominated by stem-group forms, and the

Ordovician record by crown-group forms, with the stem lineages having by this time largely disappeared (G. E. Budd and S. Jensen, in preparation).

(6) Finally, this analysis suggests several further lines for research. First, the recognition that many or most Cambrian taxa lie within the stem groups of phyla or even deeper in the metazoan tree offers considerable hope that a morphological, functional and ecological picture of phyletic origins may be built up from the fossil record, despite the general pessimism that is generally expressed about this possibility (Knoll & Carroll, 1999). The tendency to hide such problematic forms in extinct ‘phyla’ obscures the logically necessary point that such forms must have stem- or crown-group relationships to extant taxa. Indeed, this task of systematization has for some phyla already begun. Theories of the origins of phyla would in such a case be forced to consider the functional morphology and adaptive assembly of body-plan features, rather than, as is common presently, assuming that large morphological gaps in the extant fauna require unusual ‘macroevolutionary’ mechanisms to explain them (another instance of the ‘retrospective fallacy’). Secondly, the constant importance of functional morphology in shaping the possible routes and contexts that body-plan evolution could have taken place in suggests that more research be directed towards understanding the shifts in system functionality that take place, during especially size change. Such analysis might lead to a more precise understanding of what limitations are placed on body-plan evolution – perhaps ancestral bilaterians needed to be considerably greater than 1 cm long, for example. Thirdly, this work suggests that the origins of body plans are unlikely to be understood fully until good phylogenies of extant members of clades are available, in particular with reference to reconstructing the features present in the ‘ground plans’ of the phyla.

VII. ACKNOWLEDGMENTS

We are most grateful to the many colleagues who have generously discussed and contributed data to various aspects of this work. In particular, Ruth Dewel has provided many stimulating ideas. We would also like to thank Simon Conway Morris, Andrew Smith, Paul Taylor, John S. Peel, Lars Holmer, Kevin Peterson, Richard Fortey, Andrew Knoll, Malgorzata Moczydlowska-Vidal, Fredrik Ronquist, Nick Butterfield, Lennart Olsson, Joakim Eriksson, Allen Collins, James Gehling, Bruce Runnegar and Mary Droser for discussion

and help, and for their tolerance of our views where they have differed markedly from their own. J. S. Peel, S. Conway Morris, Hou Xiangjuang and J. Bergström kindly provided figures as detailed in the figure captions. D. H. Erwin kindly read and commented on a previous draft. This work was funded by the Swedish Natural Science Research Council (G.E.B.) and the Natural Environment Research Council, UK (S.J.). Cambridge Earth Sciences Publication No. 5749.

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